Version 9.21

VORTEX

A Stochastic Simulation of the Extinction Process

User's Manual

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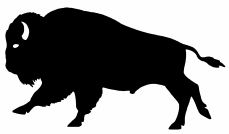

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Lacy, R.C. 2000. Considering threats to the viability of small populations using individual-based models. Ecological Bulletins 48:39-51. 139

Chapter

1

Introduction

VORTEX is an individual-based simulation model for population viability analysis (PVA). This program will help you understand the effects of deterministic forces as well as demographic, environmental, and genetic stochastic (or random) events on the dynamics of wildlife populations. *VORTEX* models population dynamics as discrete, sequential events (e.g., births, deaths, catastrophes, etc.) that occur according to defined probabilities. The probabilities of events are modeled as constants or as random variables that follow specified distributions. Since the growth or decline of a simulated population is strongly influenced by these random events, separate model iterations or "runs" using the exact same input parameters will produce different results. Consequently, the model is repeated many times to reveal the distribution of fates that the population might experience under a given set of input conditions.

VORTEX simulates a population by stepping through a series of events that describe the typical life cycle of sexually reproducing, diploid organisms. The program was written originally to model mammalian and avian populations, but its capabilities have improved so that it can now be used for modeling some reptiles and amphibians and perhaps could be used for fish, invertebrates, or even plants—if they have relatively low fecundity or could be modeled as if they do.

The purpose of this manual is to provide you with complete instructions on how to install and use *VORTEX*. It is not intended as a primer on population biology; you must be conversant with this discipline to use the program appropriately and effectively. In addition, you must know something about the biology of the species that you intend to model. You should gather as much information as possible in order for *VORTEX* simulations to be meaningful. The old computer adage of "garbage in, garbage out" is aptly applied to population viability analysis, and PVA using *VORTEX* is certainly no exception. Having said this, it is important to recognize that many of the questions *VORTEX* asks as you construct your population model cannot be answered simply because the data do not exist. The only recourse that you will have is to enter your best guess. Oftentimes, your best guess is not yours alone; most (if not all) population viability analyses have succeeded through the efforts of many. Two or more heads are usually better than one when you find yourself faced with a *VORTEX* question with no known answer. Further information about *VORTEX* and the structure of the model is provided in publications reprinted as appendices to this manual.

What's New in *VORTEX* Version 9?

The biggest change from prior versions of *VORTEX* is that the program is now a Windows application. Although the user interface is now totally new, experienced *VORTEX* users will quickly recognize that the content of the program (the input variables, the information output, etc.) is still very much like that of the old MS-DOS versions of *VORTEX*. In fact, unless you invoke one of the few new features of the overall model, results generated by the Windows version should match (except for stochastic uncertainty) the results produced by the earlier DOS versions.

You cannot directly import input files from prior (DOS) versions of *VORTEX* into version 9. However, for an experienced *VORTEX* user, it usually takes only a few minutes to re-enter the input values from a prior analysis. Attempts will be made to make future updated versions of *VORTEX* capable of importing projects from all previous Windows versions of the program (version 9.0 and higher).

The user interface for entering input values, running simulations, seeing tabular and graphical representations of output, and obtaining help are clearly very different in the Windows *VORTEX* than in the earlier DOS versions. The easiest way to get a feel for these differences is to open the program and explore it. A "Quick Tour" of the new program is provided in Chapter 2, and new users are encouraged to use it to become more familiar with *VORTEX* version 9.

In addition to the switch to a Windows interface, there have been a few upgrades to the underlying population biology model available in *VORTEX*. The most significant one (and the one that would be most noticeable to users) is the availability now of "Individual State" variables. These optional variables allow you to create descriptors of states or characteristics of individuals in the populations. These states can be anything you want them to be – for example, dominance status, body condition, location on the landscape, or territory quality. If you specify Individual State variables, then you must define how they are initially determined for each individual at the outset of the simulation and when individuals are born, and how an individual's state can change across years. Once defined, these variables can be used as modifiers of any of the demographic rates – such as probability of breeding, litter size, mortality, susceptibility to catastrophes, and dispersal. Using this feature of the *VORTEX* model, you can create very complex and detailed models of population dynamics. (For example, breeding could be function of the dominance status of individuals, which could in turn be determined by maternal dominance status and a random component.) However, we will not hide the fact that appropriate and wise use of Individual State variables can be very difficult, and we strongly caution new *VORTEX* users to stay away from creating such complex models.

How to Use This Manual

By following the detailed instructions provided in the *VORTEX User's Manual*, you should be able to construct surprisingly complex models of stochastic growth dynamics of wildlife populations. In addition to this instruction, the *User's Manual* provides you with supplementary information designed to help you get the most out of *VORTEX* and to see how it and related software packages are used in practical applications of conservation biology.

- Chapter 2, GETTING STARTED WITH *VORTEX*, gives you information on the program's modest system requirements and shows you how to install, run, and close the program.
- Chapter 3, CREATING A PROJECT: DATA INPUT, provides a wealth of information on the types of biological data necessary for developing a *VORTEX* population model and the mechanics of entering data into the program.
- Chapter 4, VIEWING MODEL RESULTS, describes how to view your model results, in text, tabular and graphical form and how to work with output data files to assist in effective data analysis.
- Chapter 5, USING FUNCTIONS IN *VORTEX*, presents a detailed description of how to use this major, but complex, feature.
- Appendix I, AN OVERVIEW OF POPULATION VIABILITY ANALYSIS USING *VORTEX*, gives a brief introduction to the principles of small population biology and describes in more general terms the use of population viability analysis to assist with wildlife management and endangered species recovery.

- Appendix II, LITERATURE CITED, provides a complete listing of the scientific literature referenced throughout this *User's Manual*.
- Appendix III, *VORTEX* BIBLIOGRAPHY, includes what we hope is a reasonably complete list of references to papers that discuss *VORTEX* as a tool for population viability analysis, and to those specific examples of the use of *VORTEX* in PVAs across a diverse taxonomic range. Authors wishing to have their publications listed in future editions of this manual should email the citations to help@vortex9.org.
- Appendix IV, REPRINTS, provides copies of two papers that describe in detail the structure of the *VORTEX* model and some of the concepts behind the model.

Throughout the text you will find various aids that will enhance your overall use of *VORTEX*:

Brief explanatory notes that will help you remember important points, clarify some commonly-used terms, etc.

Text boxes that will provide additional information on general concepts in population biology and genetics, statistics, and simulation modeling.

Case Studies that show you real examples of how data have been used to develop *VORTEX* simulation models. These case studies are gleaned from the many Population and Habitat Viability Assessment (PHVA) workshops conducted by CBSG over the past decade.

A Note about Regional Windows Settings

Although we cannot guarantee that *VORTEX* will work correctly with all possible configurations of MS Windows, we believe that it will adapt appropriately to most Regional Settings of date, time, and numeric formats. Throughout this manual, screen displays are shown from a system configured with the American English regional settings. For example, the '`.`' is used as the decimal delimiter (so that the number three would be shown as `3.0`). If your operating system is configured to use the '`,`' as the decimal delimiter, then you would use that format throughout *VORTEX* for input and output (so that the number three would be shown as `3,0`). Do not use any delimiter between thousands (e.g., thirty thousand would be `30000`, not `30,000` nor `30 000`, nor `30.000`). *VORTEX* will try to automatically convert input and output files to the data format specified by your Windows Regional Settings.

VORTEX Technical Support

If you are having trouble using *VORTEX* and want additional information, there are a number of resources available to you. Be advised, however, that CBSG is unable to provide the kind of technical support you have come to expect (but rarely receive!) from large software companies. In this context, the phrase "you get what you pay for" is particularly appropriate. *VORTEX* is provided on the Internet free of charge because of our commitment to promoting the use of science in the service of biodiversity conservation. Significant resources have been provided over the years by the Chicago Zoological Society and the CBSG to support the development and continual improvement of *VORTEX*. Neither organization recovers these costs of development, nor receives any funding to provide ongoing support to *VORTEX* users.

Nevertheless, we are committed to doing everything we can to help you get the most out of your *VORTEX* modeling experience. Towards this end, we suggest the following support options:

- This *User's Manual*. We hope that we have provided you with all of the information necessary to navigate your way through the program.
- Tooltips and Input Prompts. Most icons, commands, menus, and input boxes have tooltips that pop up with explanatory messages when the cursor is paused over them. In addition, during input, prompts will appear at the bottom of the window when the user clicks on a data entry box.
- On-screen Help. Chapters 1-5 of this manual are provided in the Help menu of the program.
- The *VORTEX* Listserver. To help *VORTEX* users in their use of the program for PVA, a *VORTEX* Users email discussion group (Listserve) has been established. The *VORTEX* Listserve facilitates the exchange of ideas, questions, answers, and suggestions among the many users of *VORTEX*. The listserve also provides a medium for announcing updates, bug fixes, and suggestions provided by CBSG or by the program's developer. To get information about the listserve, or to subscribe, go to **https://listhost.uchicago.edu/mailman/listinfo/vortex**. Because there is no registration of *VORTEX* users, the listserve is only way we can assure that users will hear about updates, bug fixes, and other announcements.
- *VORTEX* on the Web. Explore the *VORTEX* home page at **http://www.vortex9.org/vortex.html** to download updated programs or documentation files, to report program bugs, or to obtain other information pertinent to the effective use of *VORTEX*.
- Contact the CBSG Office. As a last resort, if you are unable to solve your problem by the means suggested above, you can reach the CBSG Office directly to get help. Our contact information is: Telephone: 1-952-997-9800; Fax: 1-952-432-2757; E-mail: office@cbsg.org.

We urge you to read the entire *User's Manual* not only to better your understanding of *VORTEX*, but also to enhance your appreciation of the perils facing small populations of threatened wildlife. For a more in-depth treatment of population viability analysis and models for use in risk assessment, we recommend Starfield and Bleloch (1986) and Burgman et al. (1993) as excellent introductions to these topics.

A Note about Cost

Vortex is provided free of charge because of the commitment of the Chicago Zoological Society to making it widely available to further biodiversity conservation. Similarly, the manual, developed by the CBSG, is provided for downloading because the CBSG cares about saving species and their habitats. However, the initial development and continuing improvement of the software and manual do represent a significant commitment by these conservation organizations. The rate at which improvements can be made is determined by the resources available to support that work.

If your budget allows it, please consider making a donation to support the further development of Vortex. If you find the software to be especially valuable to you, consider donating perhaps US$100 (a wild guess about the investment of resources per user that have gone into Vortex), or more or less as you feel is appropriate.

If you find the manual to be especially helpful, consider donating to the CBSG. As a side benefit to US tax-payers, donations to either the Chicago Zoological Society or the CBSG are tax-deductible. Donations to the Chicago Zoological Society should be as a check written to the Chicago Zoological Society, sent to "Vortex donation, Department of Conservation Biology, Brookfield Zoo, Brookfield, IL 60513 USA". Donations to the CBSG should be sent to "Vortex donation, CBSG, 12101 Johnny Cake Ridge Road, Apple Valley, MN 55124, USA".

Chapter

2

Getting Started with *VORTEX*

System Requirements

VORTEX version 9 was developed as a C++ program (for the simulation code) presented within an interface developed in MS Visual Basic. To our knowledge, it will install and run properly on computers with Pentium (or newer) processors running Win95, Win98, WinXP, Win2000, or WinNT operating systems. We believe that *VORTEX* will work properly with a diversity of Windows Regional settings – for example, it can use common European data formats. However, we cannot guarantee that it will work with all system configurations. At this time, the user interface of *VORTEX* is presented in American English. At a future time, versions in Spanish, German, French, or other languages may be made available.

For many analyses, *VORTEX* will use much of your computer's system resources. Faster results and better performance will be obtained if you do not try to run other large applications (such as MS Word, Excel, or Outlook) at the same time that *VORTEX* is running. The program may not run properly with less than 64 MB of system memory (RAM), and even more RAM will be required if you want to run other applications concurrently. In addition, the size of the populations that can be analyzed will be determined by the available RAM. For example, simulation of a population of 5000 living animals can require up to about 50 MB of RAM for storage of inbreeding calculations. The program requires much more memory if you include inbreeding depression in your analyses, so omitting inbreeding depression (see Chapter 3) will allow analysis of larger populations and will run much faster.

Installation

To install *VORTEX* from the CD:

> Place the *VORTEX* installation CD into the appropriate disk drive, and then run the *SETUP* program. (Either double-click on *SETUP* from Windows Explorer, or go to *START>RUN,* and then enter *D:\SETUP.EXE*, in which D: is your CD drive.)

To install *VORTEX* from the Internet:

> Go to **http://www.vortex9.org/vortex.html** and download the current version of the installation program. Save this downloaded file to any temporary directory of your hard disk or to your desktop. Double-click on the downloaded file to unzip the installation package files. Unzip them to the directory where you saved the downloaded file, or to any directory of your choosing, other than the directory to where you wish to install *VORTEX*. Run the *SETUP* program. (Either double-click on *SETUP* from Windows Explorer, or go to *START>RUN,* and then enter

C:\TEMP\SETUP.EXE, in which C:\temp is the drive and directory where you placed the installation files.)

You may want to put a short-cut to *VORTEX* on your Desktop.

VORTEX is copyrighted but not copy-protected. You can make as many copies as you wish, and you may give copies of the program to others free of charge. You may not sell the program or any components of it, or otherwise represent it as your personal property.

Running *VORTEX*

Start *VORTEX* by double-clicking on a short-cut icon, or by double-clicking on the *VORTEX* program itself. To exit the *VORTEX* program, just click on the Close button (marked by an ×) in the top right corner of the program window. before closing, the program will always prompt you to determine if you wish to save any open projects.

Size Limitations on *VORTEX* Analyses

VORTEX allocates computer memory as it needs it, depending on the characteristics of the population or metapopulation you are modeling. *VORTEX* will make optimal use of all available memory to carry out the simulations, but the available RAM on your computer may limit the size of analysis you can complete. However, there are also some absolute limits to how large or complex a simulation can be. These limits are listed below.

- Number of iterations 10000
- Duration of simulation 2000 years
- Number of populations 50
- Types of catastrophes 25
- Maximum age 250 years
- Maximum litter size 50*
- Initial population size 30000 individuals
- Carrying capacity 60000 individuals

*Only if specifying an exact distribution; see page 44 for an alternative method to increase maximum litter size.

Some combinations of parameters can require large amounts of memory. For example, if you are including inbreeding depression in your simulation, and have chosen to model it as only partially due to the presence of lethal alleles, more than 50 megabytes of memory may be required to analyze a population that reaches 5000 living animals. In these cases, it is possible that *VORTEX* will abort an analysis if there is insufficient memory available. Even if the program does not abort, it may run exceedingly slowly as each individual and its pedigree is tracked throughout its lifetime. If you have frequent problems with aborted or slow analyses, consider taking one or more of the following steps:

- Change the mechanism by which inbreeding depression is modeled. The program will run noticeably faster if the population's genetic load is due entirely to lethal as opposed to detrimental alleles.
- Construct a simpler general model. Often a large population (or metapopulation) may exist, but the real concern may be whether smaller fragments are at risk of local extirpation. *VORTEX* will simulate small populations much more rapidly than large populations or constellations of patches within a metapopulation. If local patches do not exchange migrants, analyze them separately rather than as parts of a larger, more complex metapopulation.

- Think about using a different PVA software package. If *VORTEX* is running so slowly as to cause you much grief, the types of populations you are analyzing are probably so large that the kinds of random forces modeled explicitly by *VORTEX* —demographic and environmental stochasticity, inbreeding, and genetic drift—are likely to be irrelevant to the population growth dynamics. In these cases, it may be more appropriate to use a population-based model such as one of the packages in the RAMAS family of software (these are produced and distributed by Applied Biomathematics, Setauket, NY), or to use analytical methods (e.g., life-table analysis) that exclude most or all stochastic factors entirely.

Box A: Is *VORTEX* the Best PVA Model for Your Analysis?

Different PVA models have different strengths and weaknesses with respect to what kinds of life histories they can model, what range of processes can be examined, what aspects of population dynamics are modeled well, and how easy they are to use for different analyses. Below is a list of some considerations for evaluating whether *VORTEX* is more or less appropriate for your analysis. While they are certainly not hard and fast rules, they should help you make informed decisions about how to best conduct your analysis.

***VORTEX* may be less appropriate or may not be needed**	***VORTEX* is more appropriate and may be necessary**
High fecundity	Low fecundity
Short lifespan	Long lifespan
Polyploid	Diploid
Genetic effects of little interest	Changes in genetic variation of interest
Local population (N) > 500	Local population (N) < 500
> 20 populations modeled	< 20 populations modeled
Demographic rates not estimable (only population growth trajectories known)	Age-specific fecundity and survival rates estimable
Stage- or size-dependent demography	Age-dependent fecundity and survival rates
Demographic rate fluctuations not estimable	Fluctuations in rates can be estimated
No catastrophic events of interest	Catastrophic events modeled
Only polygamous breeding	Polygamous or monogamous breeding
Random breeding	Some adults excluded from breeding
	Non-random distribution of fecundity
Population starts at stable age distribution	Starting population not at stable age distribution
Constant sex ratio	Unequal sex ratio
No trends in habitat expected	Trends projected in habitat quality or area
No manipulation of animal numbers	Managed removal, supplementation, or translocation
Fish, amphibian, invertebrate, or plant	Bird, mammal, or reptile
You have lots of money (for buying software)	You have lots of time (for running analyses and summarizing results)

Getting Around in *VORTEX*

Your work in *VORTEX* will be structured as Projects and Scenarios. A Project will contain all your input, output, and notes about a case that you are exploring. Often, a Project will contain all the analyses about a given species or population. You could split your analyses of a species among multiple Projects, but that would preclude you from easily copying input, results, or settings among the separate Projects containing your work. On the other hand, there is no advantage to combining work on different species or cases into one Project, and it may be more useful and less confusing to keep distinct PVAs in separate *VORTEX* Projects. It is probably a good idea to specify a new directory for storing each Project (and this is the default in *VORTEX*), although you can store all your work in one directory if you wish.

Each Scenario within a Project contains a discrete set of input values and (if it has been run) output. Thus, for a given species (Project) you may decide to test several or even many different Scenarios, each of which would have an alternative set of input values, representing an alternative view of the population. For example, different Scenarios may represent various plausible input values to be explored during sensitivity testing, or may represent alternative management options that might be applied to a population.

The *VORTEX* interface has separate screens (windows) or tabs for Project Settings, Simulation Input, Text Output, Graphs and Tables, and a Project Report. Each of these are specific to an open Project, and you can toggle among the Scenarios of a Project within the input and output screens. You can open concurrently multiple *VORTEX* Projects within a *VORTEX* session, although there may only rarely be cases in which it is useful to have more than one Project open at the same time.

A *caution*: It is almost inevitable that *VORTEX* contains some bugs, and it may be that you will make some mistakes while working with *VORTEX*. Thus, it is possible that after you spend hours working on a *VORTEX* Project, the program will suddenly crash. It is also possible that you will accidentally change a very useful analysis into something that is worthless. It is strongly recommended that you periodically save your work, and even save it under a new name in a new directory (see below). Hard disk space is cheap – use it!

A Quick Tour of *VORTEX*

The first screen you will see when you begin a new *VORTEX* session is shown in Figure 1.

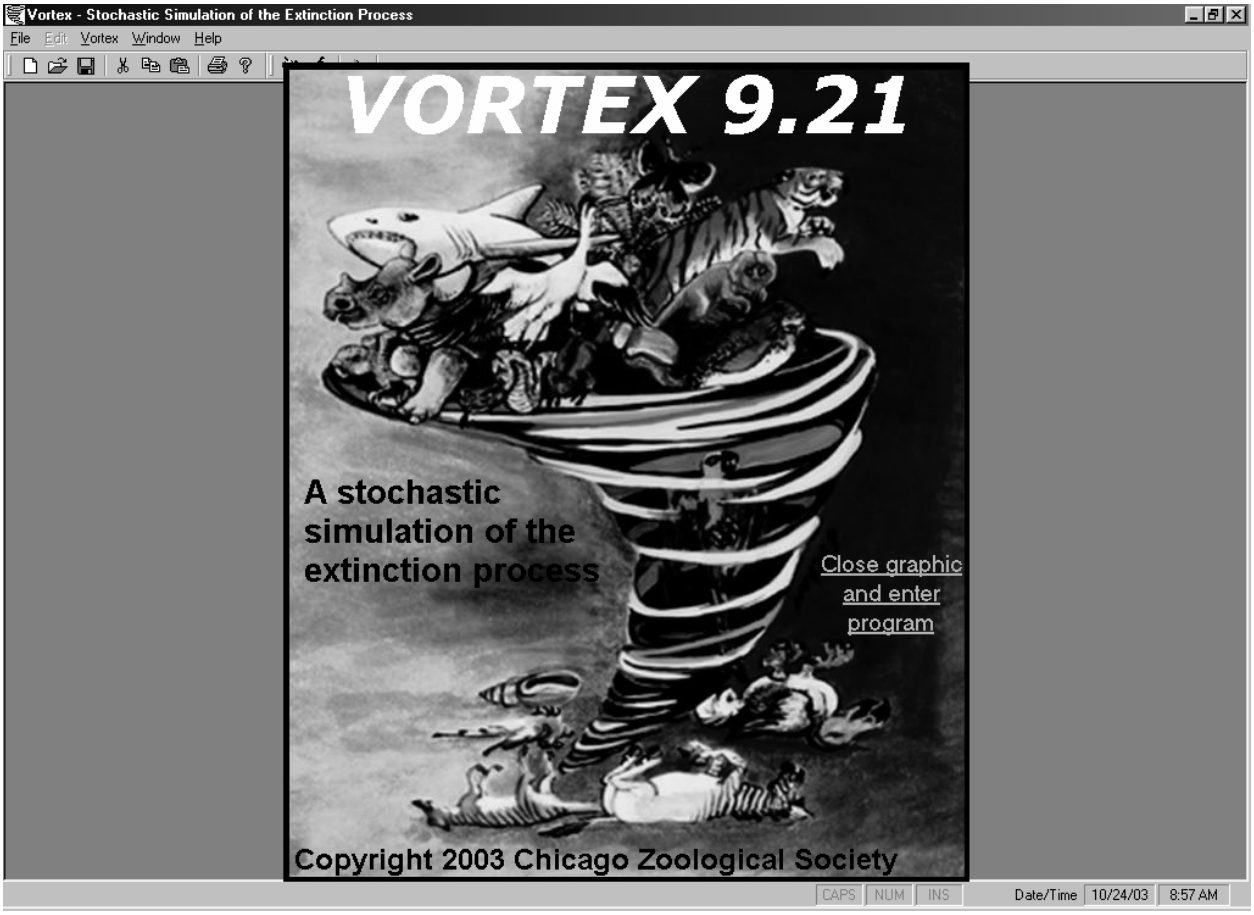

Vortex - Stochastic Simulation of the Extinction Process
File Edit Vortex Window Help
VORTEX 9.21
A stochastic simulation of the extinction process
Close graphic and enter program
Copyright 2003 Chicago Zoological Society
CAPS NUM INS
Date/Time 10/24/03 8:57 AM

Figure 1. The Vortex opening screen

After admiring this artistic representation of the extinction vortex, and appreciating the fact that the Chicago Zoological Society devoted a lot of resources to develop *VORTEX* for your use, click on the "Close graphic …" message to enter the program.

The next screen, shown in Figure 2, asks what Project you wish to open. (Note: in Figure 2, and many subsequent figures, the image shown is just the sub-window that is relevant to the point being made.) Select the Open Project tab, so that we can use an existing sample Project. A number of sample projects are copied into the Projects subdirectory when you install *VORTEX*. More sample projects will be made available at http://www.vortex9.org/vortex.html, and we encourage users to contribute their project files to this site so that others may explore those data sets.

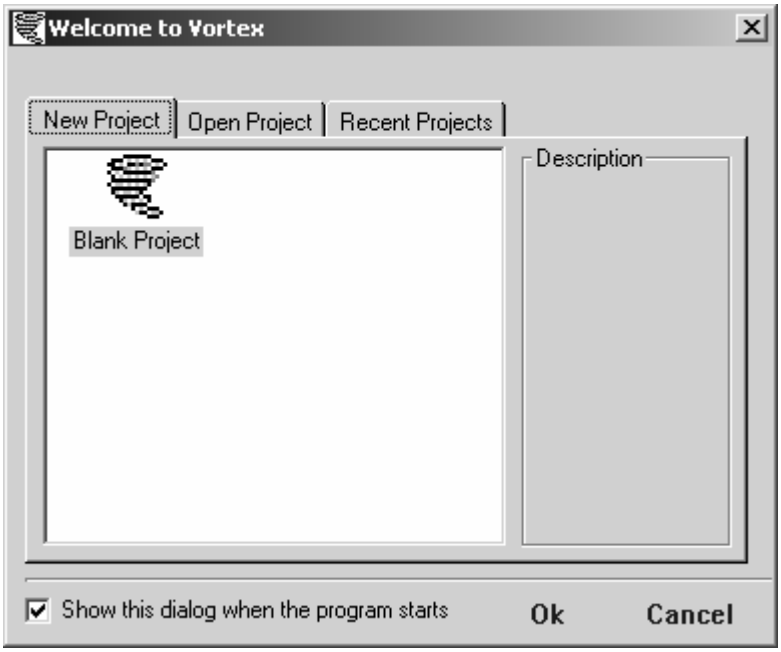


Figure 2. The dialog box for starting a Project.

Figure 3 shows the dialog box for opening an existing Project. This screen may look a little different on your computer, depending on where you installed the *VORTEX* program. Navigate to the \ZPG directory and then select the ZPG Project by double-clicking on the ZPG.vpj file, or single-clicking on it and then selecting OK. Note that windows in *VORTEX* can usually be resized or moved with the cursor.

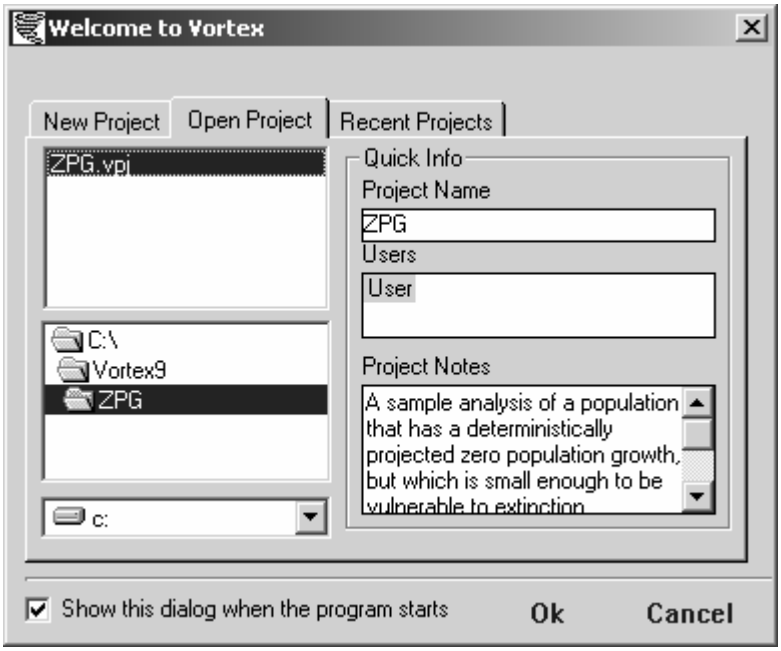


Figure 3. The dialog box for opening an existing Project.

The ZPG Project does not represent any particular species. It has a set of input values that define a population that would have an expected long-term zero population growth (r = 0.0), based on the mean birth and death rates as modified by occasional catastrophes. This projection of zero population growth is dependent upon an assumption that stochastic processes – such as demographic stochasticity, temporary

mate limitation, inbreeding, and annual fluctuations ("environmental variation") – do not reduce mean population performance. The population size in this case, however, is low enough that these stochastic processes are important impacts on the population, causing it to be unstable, often decline, and be highly vulnerable to extinction (as we will see). The ZPG Project has the same input values as the default values in the earlier DOS versions of *VORTEX*.

When you open a Project, *VORTEX* opens a screen that shows the Project Settings interface and the tabs for the other screens – Simulation Input, Text Output, Graphs and Tables, and Project Report (Figure 4). On the Project Settings screen, you can specify a different Project name, enter the names of any collaborators, and add any Project Notes text that you wish to describe your Project. It is wise to take the time to document your work by typing Project Notes and, on a screen you will see later, on Input Notes. At the time you are working, it may be seem obvious what decisions you were making when you created your Project. However, months later it may be very difficult for you (or others) to recall what led you to design the Project as you did. If you want ever to go back to a Project, take the time now to document your work within the *VORTEX* Project (see Chapter 3 for more information on entering Input Notes).

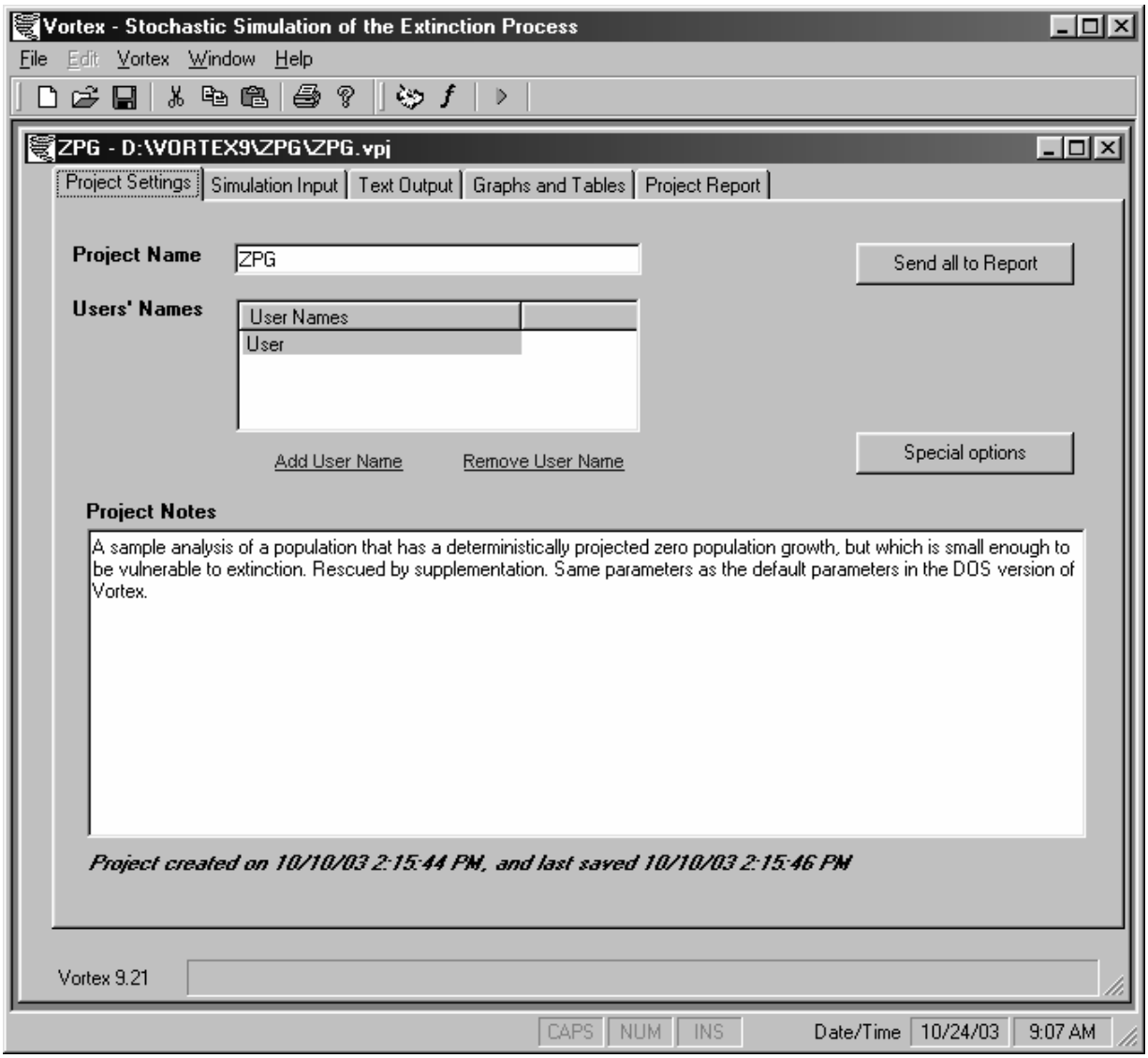

Vortex - Stochastic Simulation of the Extinction Process
File Edit Vortex Window Help
ZPG - D:\VORTEX9\ZPG\ZPG.vpj
Project Settings
Simulation Input
Text Output
Graphs and Tables
Project Report
Project Name
ZPG
Send all to Report
Users' Names
User Names
User
Add User Name
Remove User Name
Special options
Project Notes
A sample analysis of a population that has a deterministically projected zero population growth, but which is small enough to be vulnerable to extinction. Rescued by supplementation. Same parameters as the default parameters in the DOS version of Vortex.
Project created on 10/10/03 2:15:44 PM, and last saved 10/10/03 2:15:46 PM
Vortex 9.21
CAPS
NUM
INS
Date/Time
10/24/03
9:07 AM

Figure 4. The Project window.

Get into the habit of adding Notes to your Projects to document what you are doing. You will be glad that you did when you later need to tell others what you did in your analyses.

Also on the Project Settings screen is a button that will send the Project Settings information to your Project Report. Your Report is a note pad utility (much like MS Notepad) that lets you build documentation of your Project. We will take a look at the Project Report soon; for now, click on the "Send all to Report" button to capture the settings information in your Report.

Send information to your Report whenever you think that you may want it documented. It is easy to delete parts of the Report, but it is hard later to see something that you never sent !

The last item on the Project Settings screen is a Special Options button. These options are ones that most users will never need to use, so we won't look at them now. Click now on the Simulation Input tab, to take you to the screen shown in Figure 5.

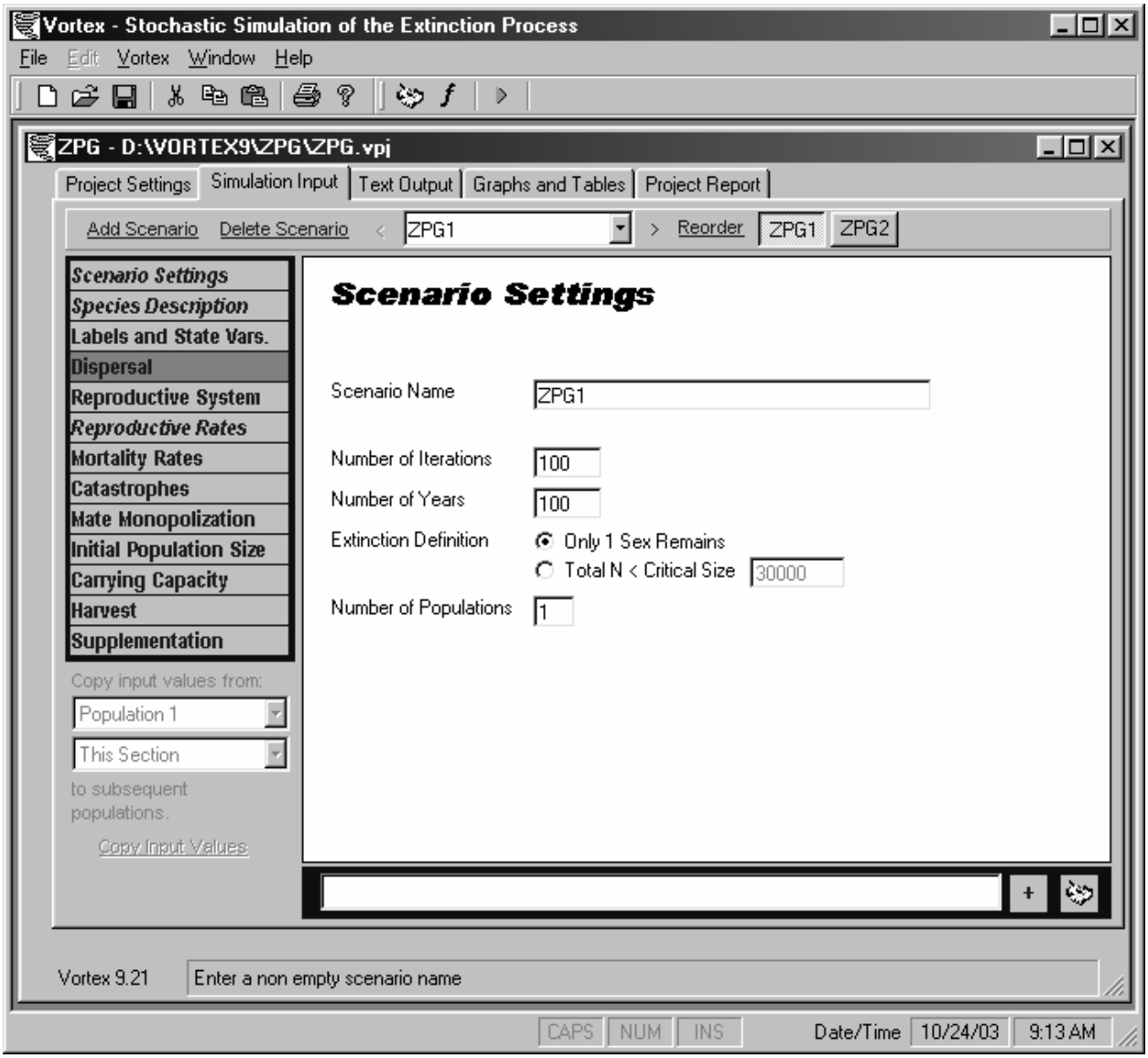


Figure 5. The Simulation Input window.

Simulation Input is arranged as 13 screens that each request values for a section of input parameters ("Scenario Settings", "Species Description", etc.). Clicking on one of the section labels in the list on the left side of the screen takes you to that section of input. Within a section, it does not matter what order you enter values, and the input sections can be accessed in any order you wish. However, it makes sense to enter values in the order they appear in the program, so that you don't forget to specify some critical value. In addition, some input sections will use values already entered from prior sections to compute useful values (such as the stable age distribution) during input. Notice that one section label, "Dispersal Rates", is greyed out and disabled. That is because the current Scenario has only one population, so there can be no dispersal among populations. Similarly, some other sections and individual input boxes will become disabled if values you have specified would make that section meaningless.

Take a quick look at the data input boxes on the Scenario Settings screen. As you click on any box, a message will be displayed at the bottom of your screen with hints about what you need to enter into that box. Now click on the "Species Description" label on the left to take you to that input section (Figure 6). Note again that some input boxes are disabled, because they pertain only to metapopulation models.

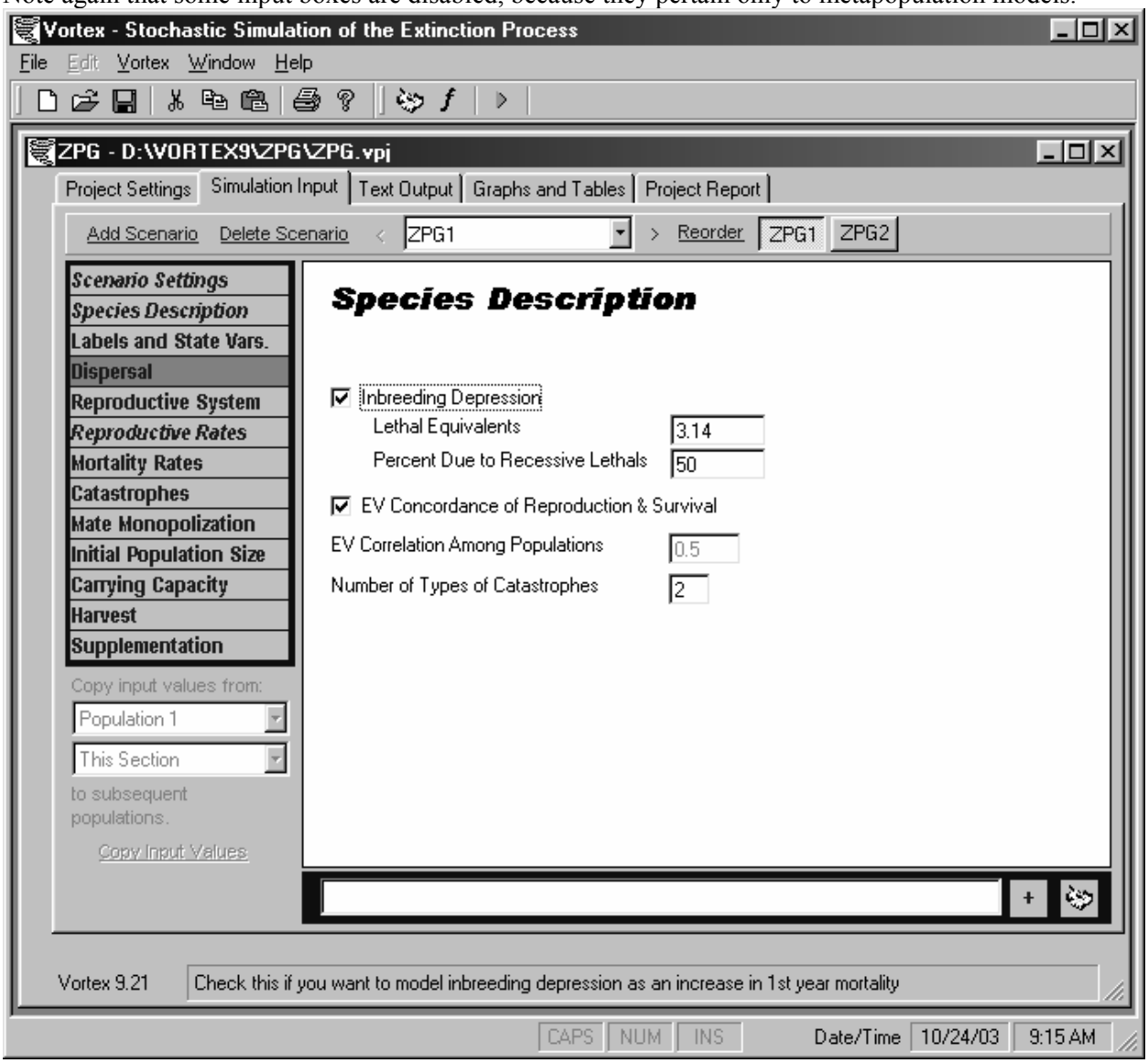


Figure 6. Species Description input section.

Step through each of the input sections, looking at the input values that are requested by *VORTEX* and the values that were entered for this ZPG Scenario. In some sections, you may need to use vertical or horizontal scroll bars to see all of the data entered. You can also make the input screens larger by clicking and dragging the corner of the window. Go now to the Catastrophes section (Figure 7).

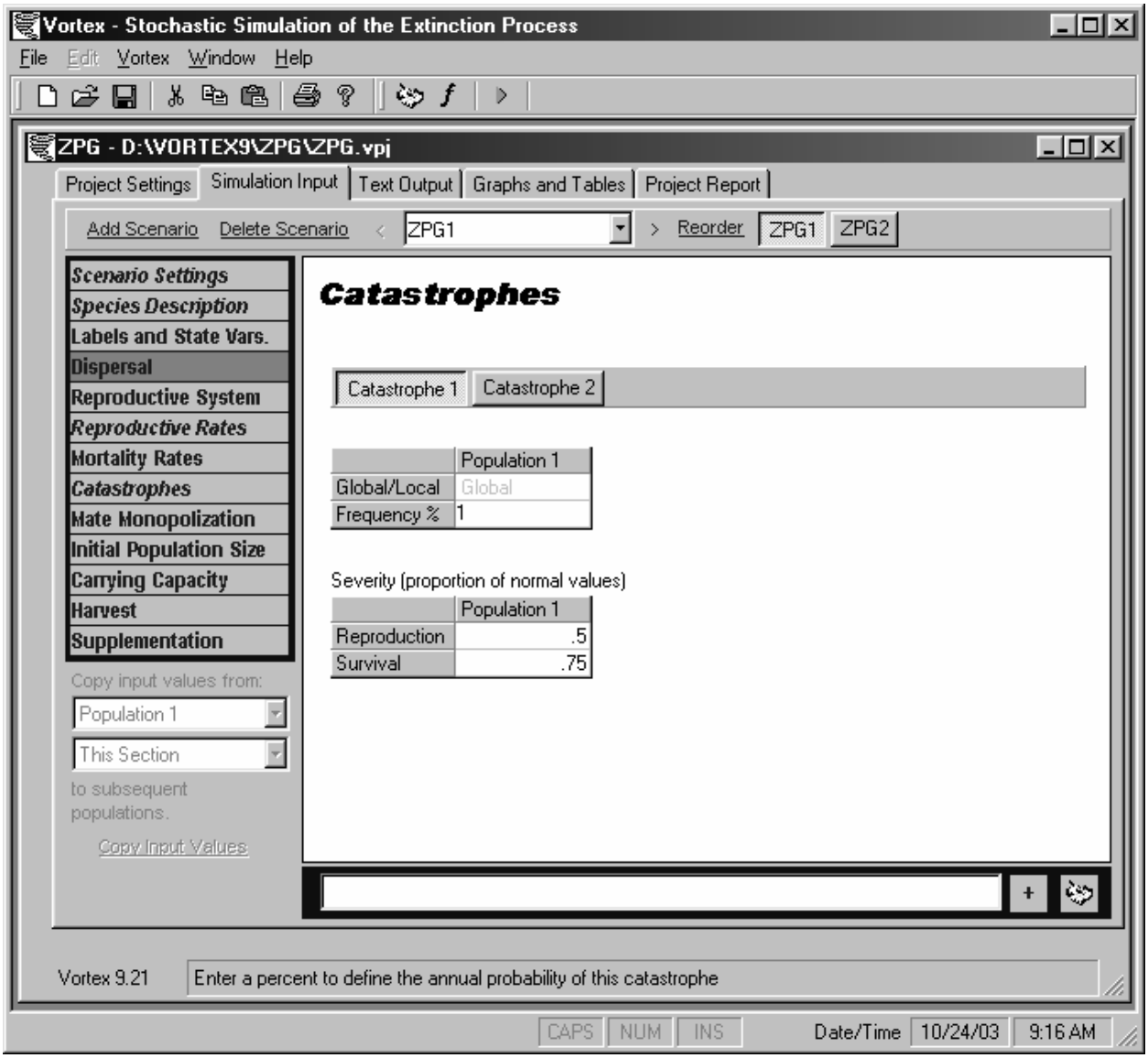


Figure 7. Catastrophes input section.

Because it was specified in the Species Description that the model should contain two types of catastrophes, the Catastrophes section has buttons to toggle between these two types. Hit the button to go to input for Catastrophe 2. In this particular Scenario, the two types of catastrophes have the same input values, so it is not obvious that you are moving between the two types (but you are).

When you are done looking through all the input sections, click on the Run icon (the green triangle on the icon bar) to open up the Run Simulation dialog box shown in Figure 8. Check the box to select Scenario ZPG1, and then click Run!

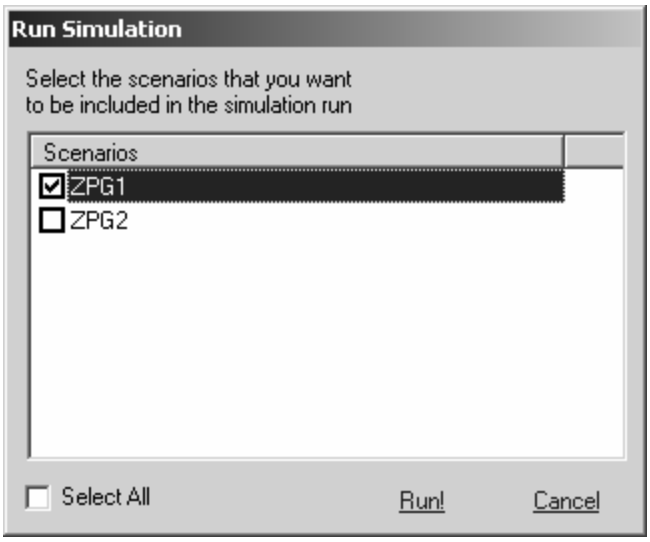


Figure 8. Run Simulation window.

Now, sit back and watch the simulation work. The lines on the screen (Figure 9) show the changing population size over 100 years for 100 different iterations for the ZPG1 Scenario. When the simulation is complete (which should take only a few seconds with this small population), the *VORTEX* Simulation display window will show a few summary statistics along the top. When you are done viewing this graphical display of the simulations, click on its close icon (✕) in the upper right corner.

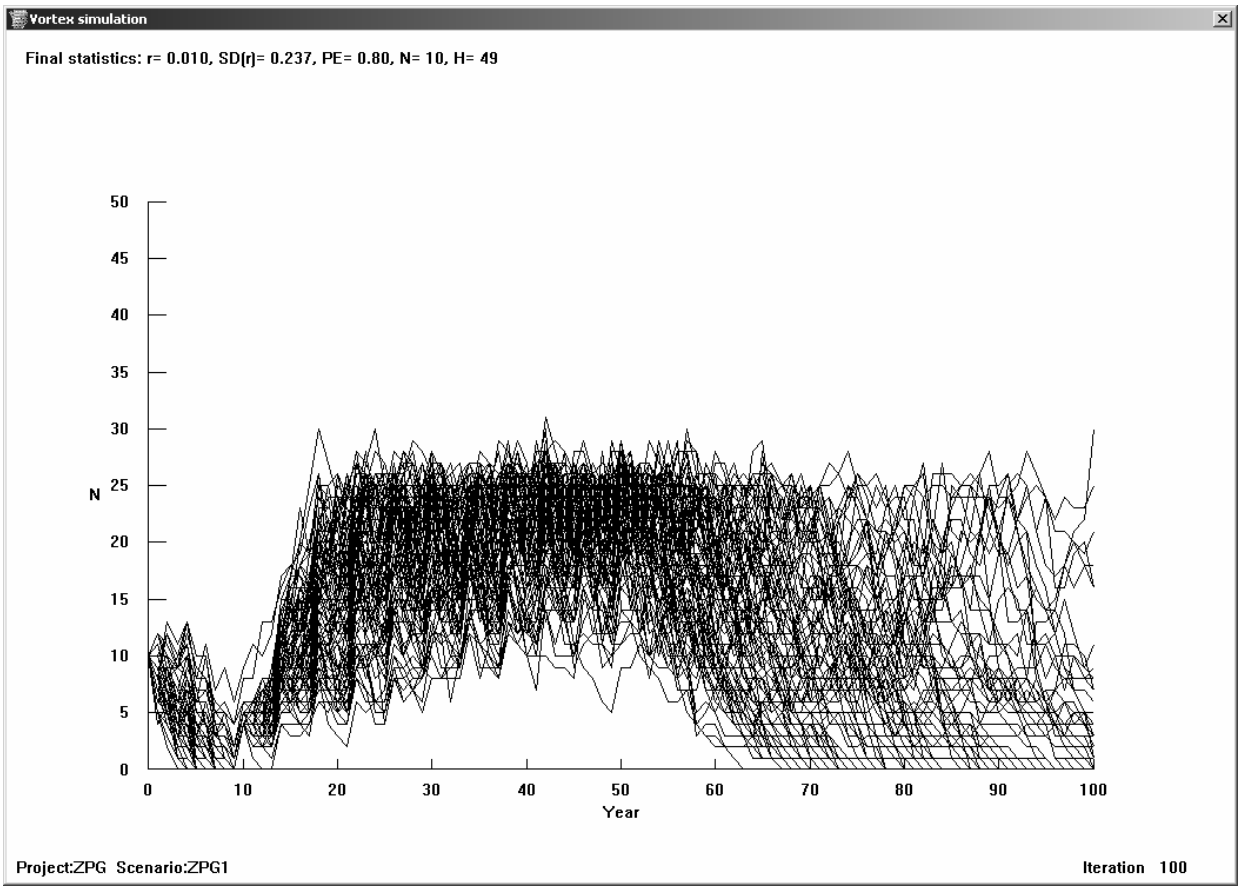


Figure 9. *VORTEX* Simulation display window.

The *VORTEX* Simulation window cannot be resized, and toggling to another window during the *VORTEX* simulations may leave you with a blank *VORTEX* Simulation window when you return to it. It is best not to move off of this window while the simulations are running. When the simulations are complete, close the window before doing anything else.

The results of the simulation you just completed are now stored with your Project on the computer. There are two modes in which you can view the results – "Text Output" and "Graphs and Tables". Go to Text Output by clicking on its tab. Within the Text Output section are four tabbed subsections – Input Summary, Deterministic Calculations, Output Summary, and Other Output (Figure 10).

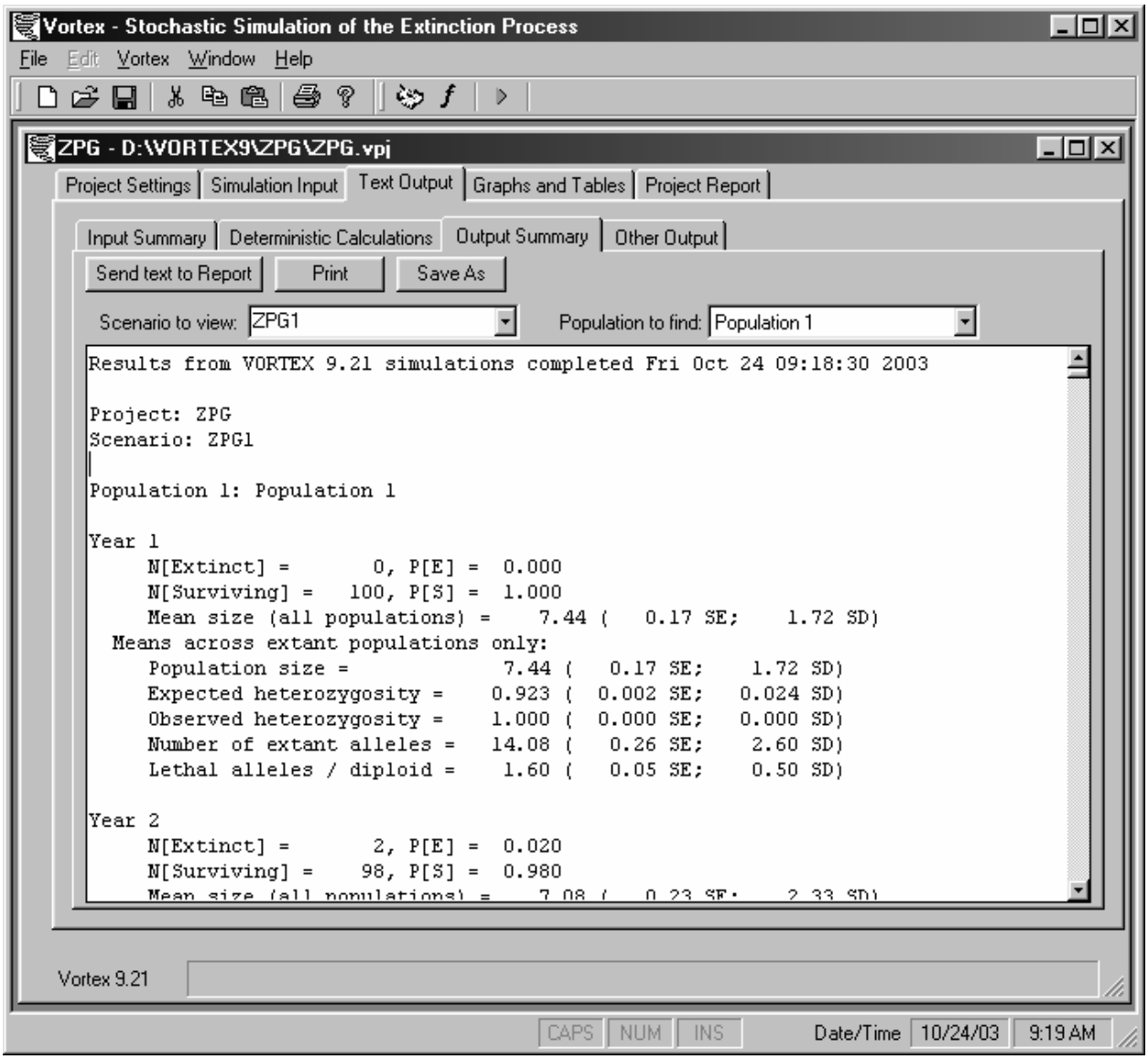

Vortex - Stochastic Simulation of the Extinction Process
File Edit Vortex Window Help
ZPG - D:\VORTEX9\ZPG\ZPG.vpj
Project Settings
Simulation Input
Text Output
Graphs and Tables
Project Report
Input Summary
Deterministic Calculations
Output Summary
Other Output
Send text to Report
Print
Save As
Scenario to view: ZPG1
Population to find: Population 1
Results from VORTEX 9.21 simulations completed Fri Oct 24 09:18:30 2003
Project: ZPG
Scenario: ZPG1
Population 1: Population 1
Year 1
N[Extinct] = 0, P[E] = 0.000
N[Surviving] = 100, P[S] = 1.000
Mean size (all populations) = 7.44 (0.17 SE; 1.72 SD)
Means across extant populations only:
Population size = 7.44 (0.17 SE; 1.72 SD)
Expected heterozygosity = 0.923 (0.002 SE; 0.024 SD)
Observed heterozygosity = 1.000 (0.000 SE; 0.000 SD)
Number of extant alleles = 14.08 (0.26 SE; 2.60 SD)
Lethal alleles / diploid = 1.60 (0.05 SE; 0.50 SD)
Year 2
N[Extinct] = 2, P[E] = 0.020
N[Surviving] = 98, P[S] = 0.980
Vortex 9.21
CAPS NUM INS Date/Time 10/24/03 9:19 AM

Figure 10. The Output Summary section of Text Output

The Input Summary section shows a text listing of all the input values used in this Scenario. Deterministic Calculations show a text summary of the deterministic population growth that would be projected from the specified mean demographic rates, if stochastic processes were not acting on the population. This section also shows a simple graph of the deterministic population trajectory. The Output Summary section gives a text description of the status of the population at each year of the simulations as well as summary

statistics for the Scenario. Other Output provides some tables with basic summary statistics for the Scenario and for each iteration. Note that the sections of Text Output provide dropdown lists to allow you to move among Scenarios and Populations. Buttons are also provided to allow you to save these texts to simple text files, to print the text summaries, or to send the summaries to the Project Report. Send the Output Summary to the Report now, so that we can view and edit it later as part of our Project Report.

All of the information shown on Text Output screens is stored automatically in text files that are placed into your project directory. While you can access and edit these files (using, for example, MS Notepad or Word), it is better to first save the text to your own files, so that they are safely stored under names that you specify and will not be overwritten if you run the simulation again.

Click now on the Graphs and Tables tab (Figure 11). The program may display a warning message stating that it could not find the data from one or more Scenarios that have not yet been run. That is OK for now (as long as you don't need yet to see the results from these other Scenarios). The Graphs and Tables section has two subsections – Data Specification and Data Graphs. Data Specification is where you will identify which results you wish to put into your table and graph.

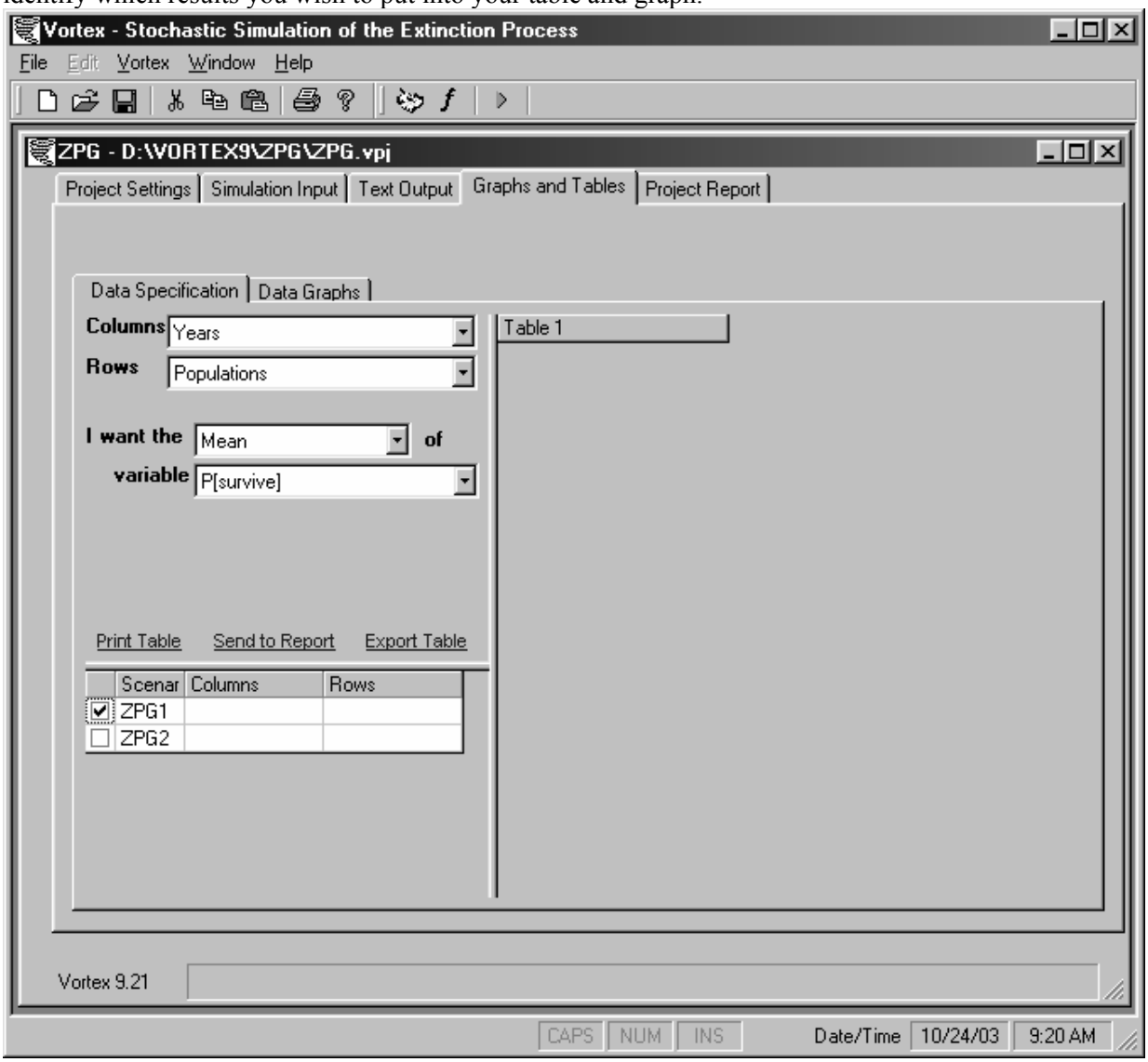


Figure 11. The Graphs and Tables window.

In the lower left list of Scenarios, make sure that ZPG1 is checked, and then double-click on the box under Columns. This will bring up a window that lets you specify which years you want to show as the columns of your table and the x-axis of your graph (Figure 12).

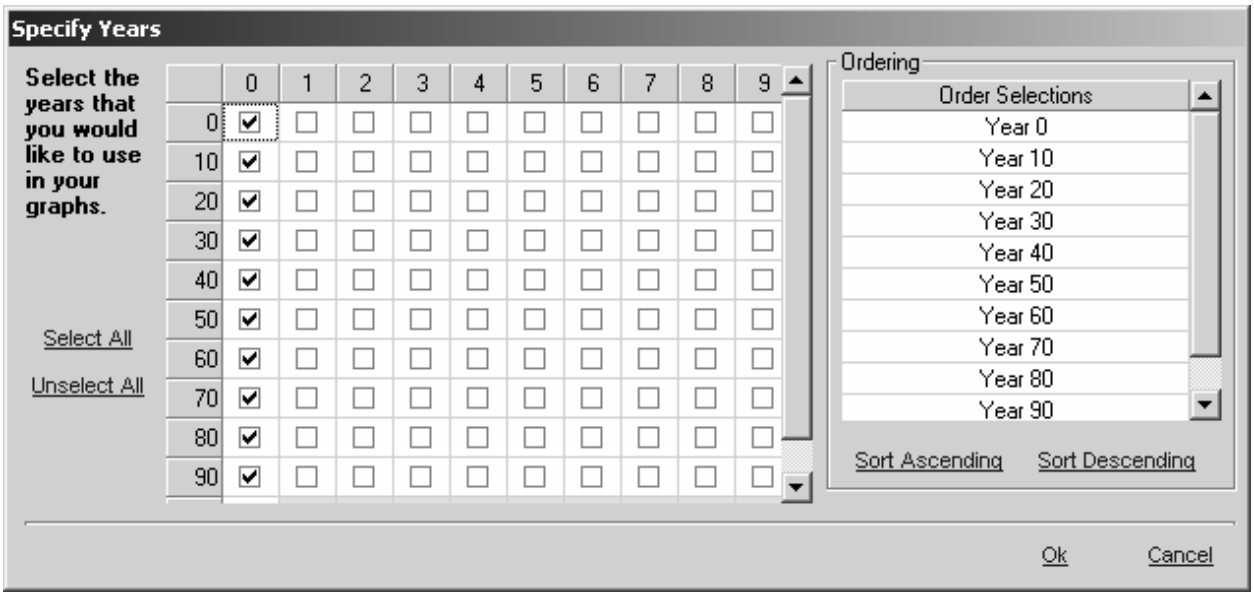


Figure 12. Specification of years as the columns for tabular output.

To specify years, you can Select All, select individual years by clicking on their boxes, or select rows (all years in a decade) or columns (years in decadal intervals) from the table. For example, to select years 0, 10, 20, …, click on the number 0 at the top of the first column. (Do this now.) The method by which years are selected may be a little confusing at first, but once you learn how it works it does allow very rapid and flexible specification of sets of years. If you add years to your selection in a non-sequential order, you will want then to sort them by clicking on one of the sort buttons on the right. After you have selected the years you want, click on OK.

When changing your selection of reporting years, you may obtain better results if you Unselect All before making your new selection rather than unchecking multiple boxes.

Next click on the box below Rows, in order to specify which populations you want to list as rows of your data table and as separate lines on the graph that will be created. The way you select populations is the same as selecting years, except that in this Scenario there is only one population so selecting it is fairly trivial. Select Population 1 and hit OK. You will see now that a table has been created, displaying one of the result statistics for the years and population(s) that you specified. With the dropdown lists in the left side of the screen, you can change the table to display other output statistics.

Change the Variable to N(all), and then hit the Data Graphs tab to show a graph of the values in the table (Figure 13). The labels, legend, and line thickness can all be changed. By right-clicking on the graph itself, you can also access a broader set of graph properties. By clicking on labels at the lower left, the graph can be sent to the Project Report (do this now), or printed, or saved as a bitmap (.bmp) file on your disk.

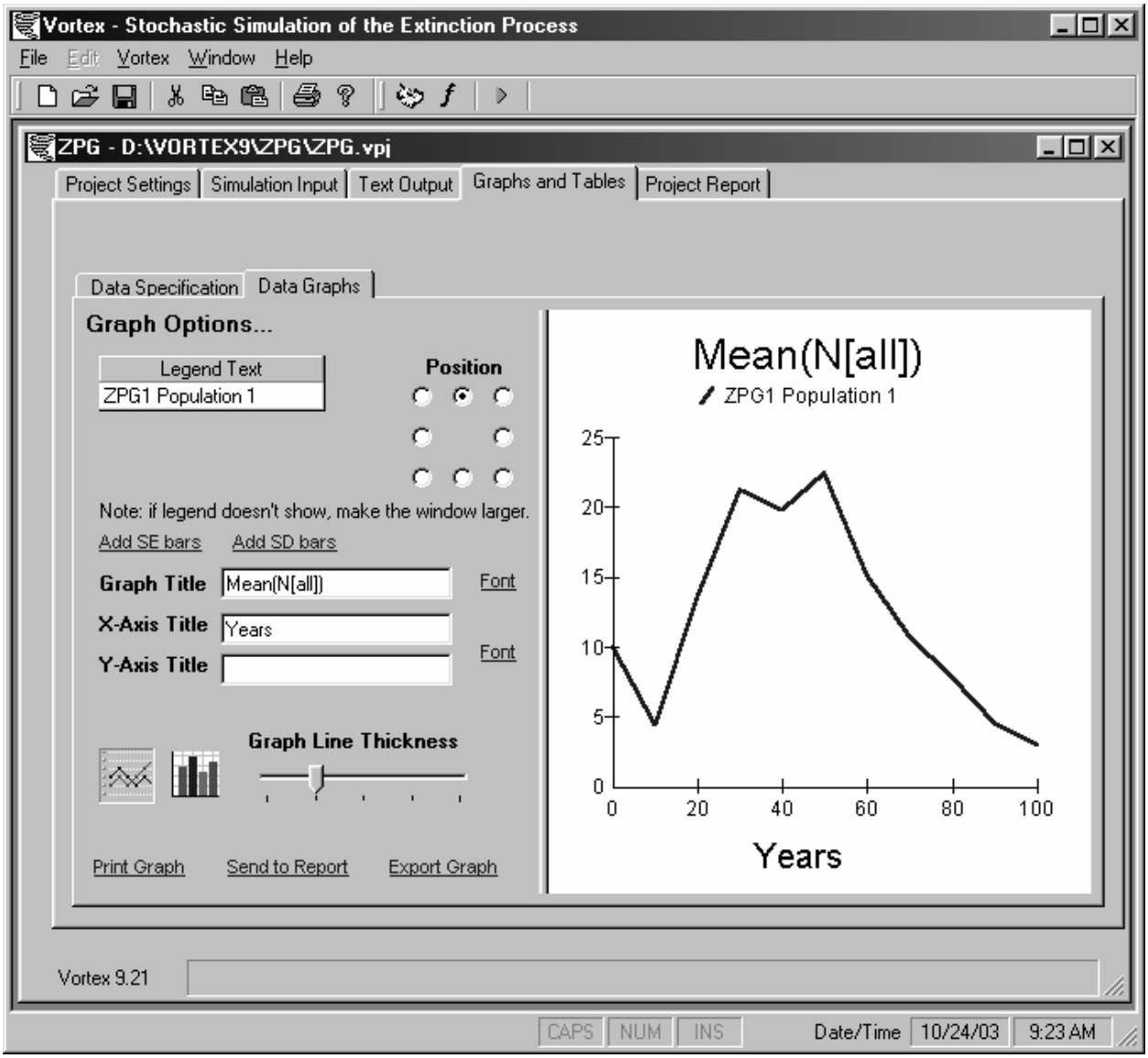


Figure 13. A Data Graph.

You should note that you have the option of adding bars to your graph to show standard errors (SE) of the means, or standard deviations (SD) across the iterations. Click on the "Add SD bars" command to see these bars.

Finally, to wrap up our Quick Tour of *VORTEX*, click on the Project Report tab. This will take you to a note pad that contains information we have sent to the Report from other screens (Figure 14). You will need to use the scroll bar or your cursor to move up and down through your Project Report. Any information in the Project Report can be edited, using standard Windows editing tools (delete, cut, paste, font settings, etc.). The Project Report is saved in Rich Text Format (and .rtf) file, and it can be edited in Word or other programs.

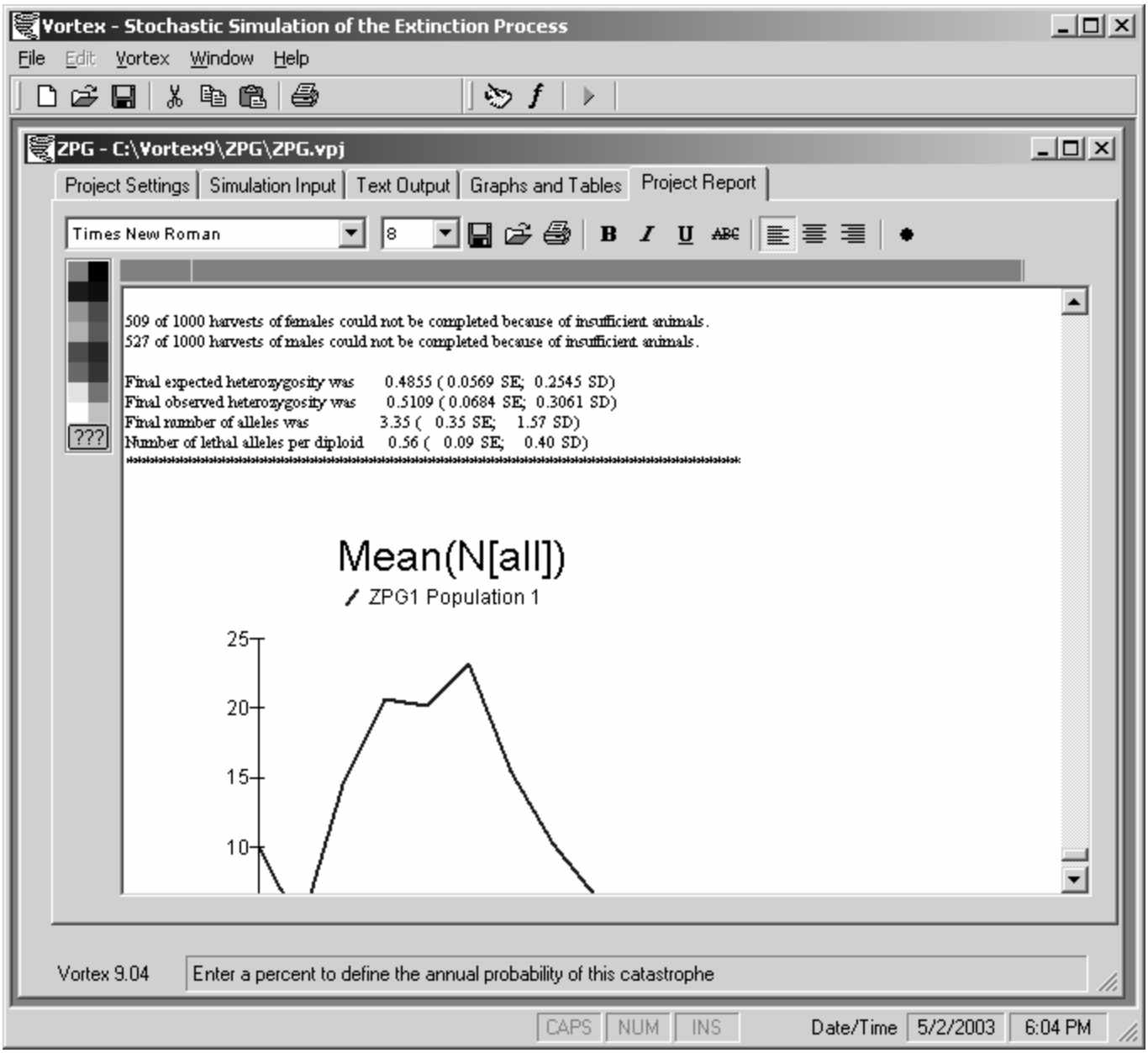

Vortex - Stochastic Simulation of the Extinction Process
File Edit Vortex Window Help
ZPG - C:\Vortex9\ZPG\ZPG.vpj
Project Settings
Simulation Input
Text Output
Graphs and Tables
Project Report
Times New Roman
8
509 of 1000 harvests of females could not be completed because of insufficient animals.
527 of 1000 harvests of males could not be completed because of insufficient animals.
Final expected heterozygosity was 0.4855 (0.0569 SE; 0.2545 SD)
Final observed heterozygosity was 0.5109 (0.0684 SE; 0.3061 SD)
Final number of alleles was 3.35 (0.35 SE; 1.57 SD)
Number of lethal alleles per diploid 0.56 (0.09 SE; 0.40 SD)
Mean(N[all])
ZPG1 Population 1
25
20
15
10
Vortex 9.04
Enter a percent to define the annual probability of this catastrophe
CAPS
NUM
INS
Date/Time
5/2/2003
6:04 PM

Figure 14. The Project Report.

You have now completed your Quick Tour of *VORTEX*, and we have looked at most of the main features of the program. Spend some time exploring other aspects of the program – change some of the input values, run additional scenarios, create some more tables and graphs. Whenever you exit *VORTEX*, the program will ask if you want to save your Project. If you do, all input, output, and report information will be saved so that it can be loaded again later.

Chapter

3

Creating a Project: Data Input

Creating a Project

When you open *VORTEX*, you must first choose whether to create a new Project or open an existing Project (Figure 15). To create a new Project, double-click on the Blank Project (or click on the "Blank Project" and then hit OK). The Open Project tab will allow you to browse to find an existing project. The Recent Projects tab will allow you to select from a list of the 10 most recent Projects that you have worked on. You can get to these same options to create a new Project or open an existing Project from either the menu or the tool bar at the top of the *VORTEX* screen.

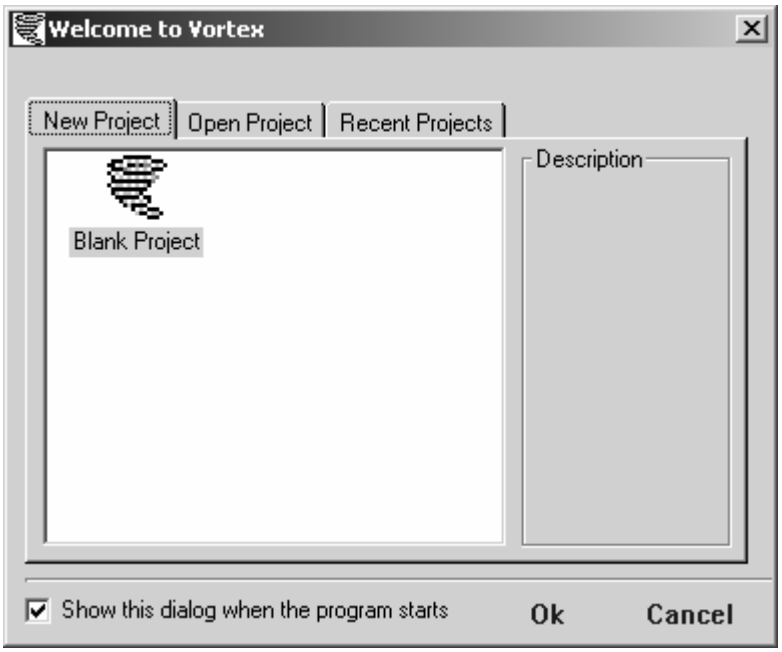


Figure 15. The welcome window for starting a *VORTEX* Project.

If you choose to start with a Blank Project, the only input values that will be pre-filled are a few that are necessary to define the basic Project and Scenario properties. It is often easier to start a new Project by opening an existing Project, and then changing those input parameters that are different. However, be sure to go through every input screen to confirm that you have set the input parameters to the new values, and be sure to save the Project under a new name. When you chose to create a new Project, you next need to specify a Project name, and you have the option of recording your name as the Project creator (Figure 16).

You can also specify the directory in which the Project files will be stored, but it usually is reasonable to accept the default, which is a subdirectory with the same name as the Project. Click OK to continue.

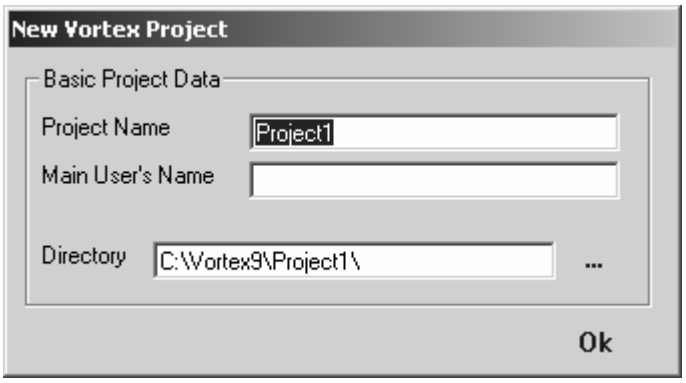


Figure 16. Dialog box for entering a new project name.

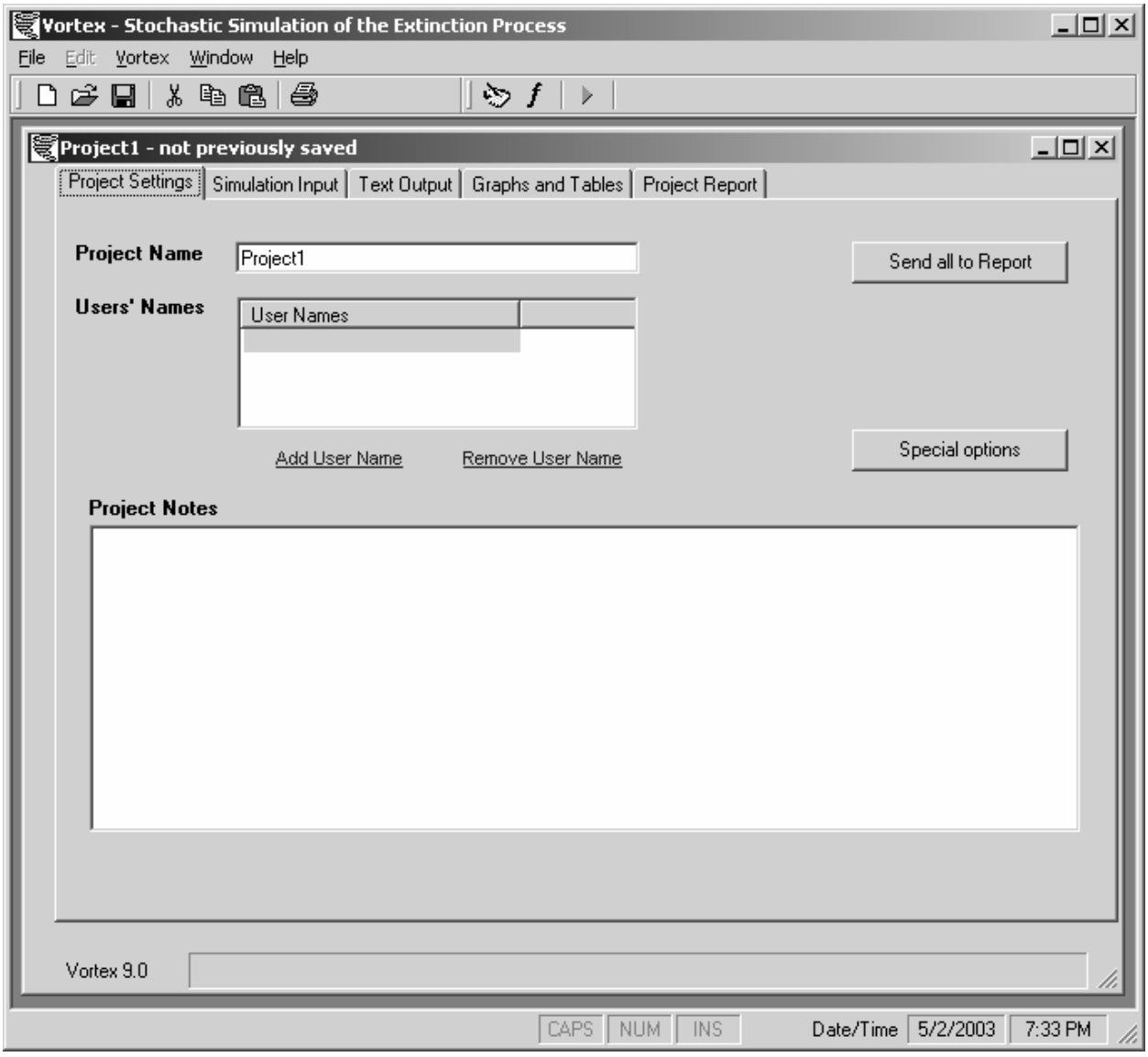


Figure 17. The Project Settings window.

In the Project Settings windows (Figure 17), you have the option of listing the names of the user team that is developing the project (this documentation may be especially helpful in workshop or classroom settings), and add any notes that you wish.

We strongly encourage you to take the time to add notes to your Project at this screen, during specification of input parameters, and in your Project Report. The extra few minutes you spend documenting your work may save you and others many hours of work later, when you try to remember what information and logic was used to create the project. Unfortunately, many PVAs are irreproducible because the authors did not fully document their work.

The Project Settings screen also has a button to send all of the settings to your Project Report (this is always a good idea, so that your settings are documented in any printed reports that you create), and another button that takes you to a screen for specifying Special Options.The Special Options will not be needed by most users. They include options to:

- change the way population sizes are graphed during the simulations,
- use the last population as a holding site for individuals that are harvested from one population and then supplemented into others (if this option is chosen, then you specify also what percent of the individuals die during this translocation among populations),
- omit the last population from metapopulation tallies (this is useful if the last population is considered an outside source for immigration into a metapopulation),
- prevent individuals from dispersing into populations that are at their carrying capacity (where the immigrant or some individual would therefore die because of the population exceeding capacity),
- define extinction as any reduction in population size (this is useful when the management goal is to prevent further population declines),
- produce files with more detailed results,
- include more neutral loci in the genetic model (useful for examining the impacts of population dynamics on genetic structure),
- invoke other options that may from time to time be made available, usually on a test basis or for special circumstances. (To use this option, you would need to know the undocumented codes for using these additional options.)

To begin entering the values for the parameters that will specify the Scenarios of your Project, click on the Simulation Input tab.

Getting Help when Entering Input Data

VORTEX will accept most of the input that you provide, as long as the values are biologically possible and within the rather wide limits set by the program (see above). When entering input data, brief hints about the values to be entered will be displayed in a line at the bottom of the Project screen. These messages appear when you click on a data entry box, and sometimes they will appear as pop-up tooltip messages when your cursor passes over a data entry box for more than a few seconds (Figure 18).

If you try to enter a value for input that is of an incorrect type (e.g., a letter when a number is required) or outside the acceptable bounds (e.g., a negative number for a mortality rate), then *VORTEX* will usually display a message that the value is invalid, and it will force you to enter a valid value before you proceed with data entry.

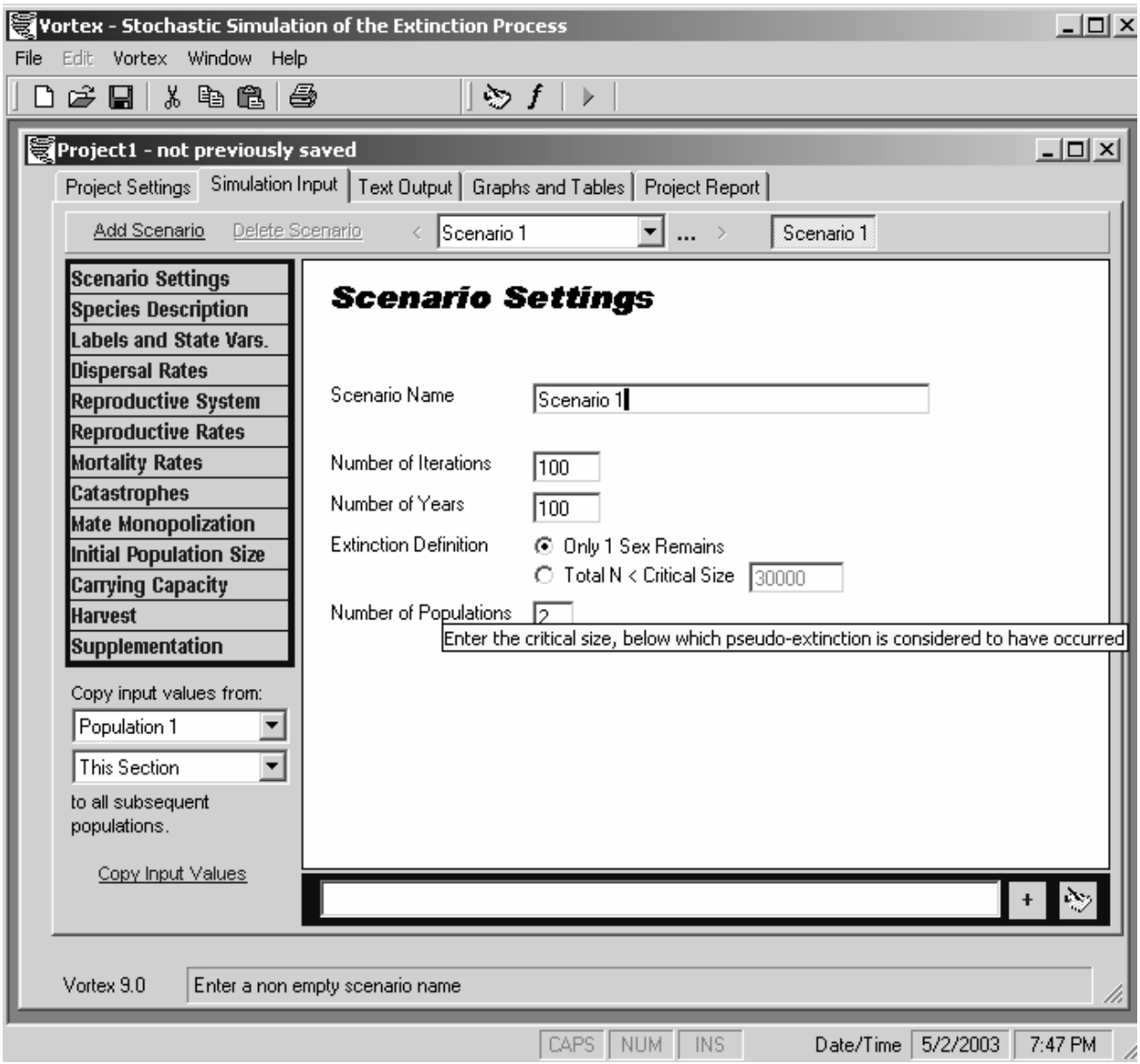


Figure 18. Scenario Settings within Input, showing a tooltip for the Extinction Definition.

It is important to remember that *VORTEX* will accept input values that are mathematically possible but biologically implausible. While *VORTEX* provides help on many data input questions you may have, such as when to enter the data as a proportion or as a percent, the ultimate responsibility for entering valid data that will result in a meaningful model rests with you, the user.

Most of the material in Chapters 1-5 of the manual is available through the Help menu of the program. Selecting "Contents" on the Help menu will take you to a Table of Contents, which provides links to each section of the Help manual. (Click on a section heading in the Table of Contents to jump to that topic in the manual.) Selecting "Context-sensitive" help from the menu or clicking on the '?' icon on the toolbar will open the Help file and jump right to the place in the file that describes the current program screen.

Documenting Your Input with Notes

Whether you are using *VORTEX* as a researcher, a wildlife manager, or a student, it is highly likely that you will need to document for others (and even for yourself when you return to a Project that had been set aside for a period of time) why you used the input values you did to create your Scenarios. When you are eager to get a Project running, it is very tempting to skip over the task of documenting the sources and reasons for your input values. However, you may save yourself later hassles if you take the time at the outset to record why program options and parameter values were chosen.

VORTEX provides a utility to attach a note with each piece of data requested as input. You can access the Input Notes by any of three methods: clicking on the Notes icon at the lower right corner of the Simulation Input screen; clicking on the same icon on the program toolbar; or directly typing into the long text box below the input window. After you type a note into the text box showing on the Simulation Input screen, hit the '+' button to add that Note to your Project, or just hit Enter. Your Note is then associated with the input parameter or question that last had cursor control. (Be careful not to enter a Note and then immediately click on another data entry box. If you didn't hit '+' or Enter, your Note will be discarded.)

When you open Input Notes by clicking on its icon, you then select the Input section input parameter for which you wish to enter a note (Figure 19). You then enter the text of your note in the box at the right.

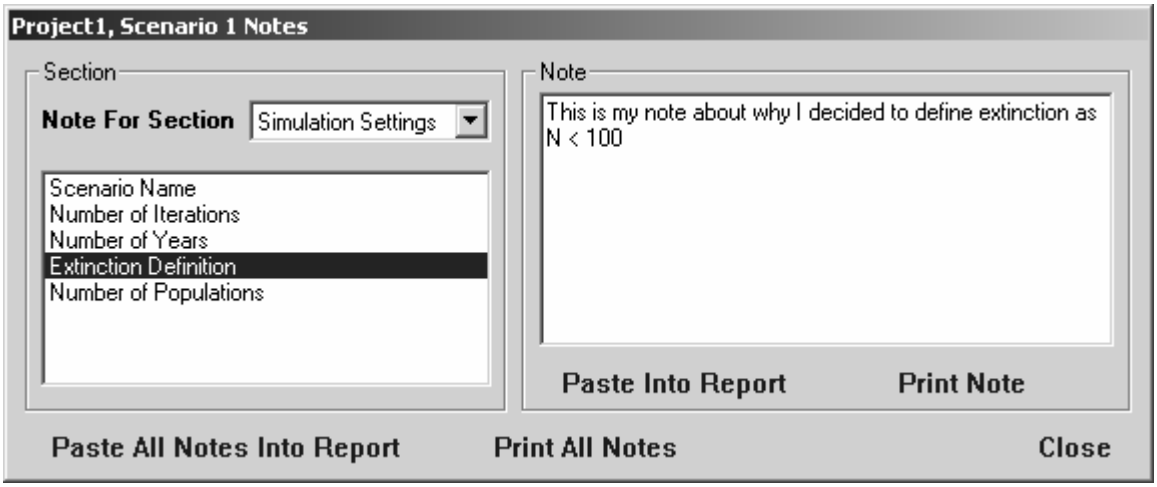


Figure 19. Input Notes pop-up utility.

As you move among input screens and boxes, the Note for the input box that is selected is displayed in the text box below the input window.

The Input Notes screen provides commands for pasting the displayed Note or All Notes into your Project Report, and for printing the displayed Note or All Notes. Thus it is easy to quickly insert your Input Notes into a report of your work. Input Notes are always saved when you save a Project.

Creating a Scenario

Input of model parameters into *VORTEX* is accomplished in 13 sections, each containing questions pertaining to a category of model parameters. You move among the input sections by clicking on their labels in the list on the left hand side of the Simulation Input screen. You can move among the sections to enter data in any order, although the list provides a logical sequence for data input. After you have visited an input section within a *VORTEX* session, the label for that section will be in italics. This may help you to quickly check whether you have completed data entry for every section.

If you jump around among input sections, you risk forgetting to visit a section, and then running models that are missing some parameters or that have values from scenarios used as templates. In addition, *VORTEX* uses answers on some early screens to complete intermediate calculations (such as the stable age distribution) that are useful when you reach later input sections.

Scenario Settings

The first data input screen you encounter when creating a Scenario asks for some basic Scenario Settings (Figure 18 above). Subsequently, you will need to step through 12 more input screens to complete the process of specifying the values for all of the input parameters needed by *VORTEX*. Below are described all the input parameters requested on these screens.

Scenario Name: Within each project you create scenarios that are defined by their sets of parameter values. As you will see, after you have defined one scenario (often a "Baseline" or "Best Guess" scenario), it is easy to create additional scenarios that change one or a few of the input values. The default scenario name for a new project is just "Scenario 1". On the Scenarios Settings screen, you should change this to a more descriptive name.

Number of Iterations: The answer to this question instructs *VORTEX* on how many times you wish to repeat the simulation, given the data that you provide in the subsequent steps. Each repetition is generally defined as a "run" or "iteration". Because *VORTEX* uses a random number generator to simulate random events in the life cycle, no two iterations will be identical. Thus, to obtain a more complete "picture" of your simulated population, you will want to generate multiple iterations of your model.

As a first step in the development of a sound population model, you may want to make sure that the simulated population is behaving in a manner that is similar to your expectations. To check this, you can limit the number of iterations to just 10 or 20. If you wish to obtain a relatively crude picture or your results, use 100 iterations. Once you are comfortable with the model and wish to obtain a more rigorous description of the simulated population's behavior, it is not excessive to enter 500 or even 1000 iterations in this field. Note that commas are not used when specifying larger numbers during the input process, even if your computer is set to use American data formats .

Number of years: How far into the future do you wish to project your population? The usual answer to this question is 100 to 200 years, although a shorter duration can be entered so that you can assess the validity of your input parameters, or to examine the short-term viability of a population. If you simulate your population for just a few decades, however, you should be aware that processes controlling population dynamics might be leading the population toward extinction but, especially for long-lived species, the final extinction may not occur until a later time. By the time that the factors influencing extinction are apparent, the process may be so far along as to be almost irreversible. One of the major advantages of PVA modeling is that it can reveal the instability of a population long before it would be apparent through field observations.

An important point to keep in mind is that *VORTEX* does not necessarily require "years" to be defined as calendar years. Rather, the program operates more broadly in terms of "time cycles". If the species you are modeling has a short generation time and life span, on the order of weeks or months—such as mice or shrews, for example—true calendar years would be an inappropriate time scale to use for modeling population dynamics. In this case, a "year" for this type of species may actually represent only one or a few months. When calculating your demographic inputs, it is vitally important that you make this adjustment consistent throughout your calculations (see Case Study I for more information).

Case Study I:

Calculating input parameters when the "time cycle" is less than one year

Consider a hypothetical rodent population where the average generation time is 180 days. In order to model this population most effectively in *VORTEX*, the user must adjust the "time cycle" to account for this shortened generation time. In this case, we will define a *VORTEX* "year" as 90 days. Consequently, events whose occurrences are typically described on an annual or per-generation basis must be redefined in terms of the new definition of "year".

For example, consider a major catastrophic flood that is thought to occur on average once every 100 years. The annual probability of occurrence, then, is 0.01. Because of the altered definition of "year", the rodent model must define the probability that this flood will occur in any given 90-day interval. The number of 90-day time cycles in a calendar year is T = 365 / 90 = 4.06. Therefore,

$$\text{Pr(flood)}_{90} = \frac{\text{Pr(flood)}_{365}}{T} = \frac{0.010}{4.06} = 0.0025.$$

The same considerations must be applied to all other demographic rates, such as mortality, age of first and last breeding, etc. In addition, appropriate migration, harvesting and supplementation rates must be established relative to the revised time cycle.

Extinction Definition:VORTEX gives you three methods to define "extinction" of your population. For most sexually reproducing species, ultimate biological extinction is assured whenever the population has declined to the point that it no longer has individuals of both sexes. In the first (and most common) choice, extinction is simply defined as the absence of at least one sex.

You also have the option to assess the probability of a population dropping below a user-defined threshold size – termed *quasi-extinction*. The use of quasi-extinction risk offers a useful alternative to the standard extinction risk. If you chose to have the simulation tally quasi-extinctions, you need to specify the threshold "critical size" below which a population is considered extinct. The simulation will, however, continue to run, as the population may grow again to a size above this threshold. Such recovery from quasi-extinction would be tallied as a recolonization event. A third option is available under Special Options on the Project Settings screen, which defines extinction as any decline in population size.

Number of Populations: VORTEX can model a single, isolated population or a complex *metapopulation* composed of up to 50 populations. A metapopulation is a group of populations which, because they often occupy fragmented, discontinuous habitat, exchange individuals with varying frequency. Note that, because of the added complexities associated with metapopulations, these models will often run considerably slower than the corresponding single-population models.

If there is no exchange of individuals among populations (i.e., dispersal) in your model, it maybe faster to run several individual simulations (with each one modeling an isolated population) instead of a more complex metapopulation model.

Enter the number of populations that comprise your metapopulation model or enter **1** for a simulation composed of a single population. If you intend to build a metapopulation model, you will later need to specify dispersal rates and some other parameters.

Species Description

The next section of input includes a set of basic questions about the species being modeled (Figure 20).

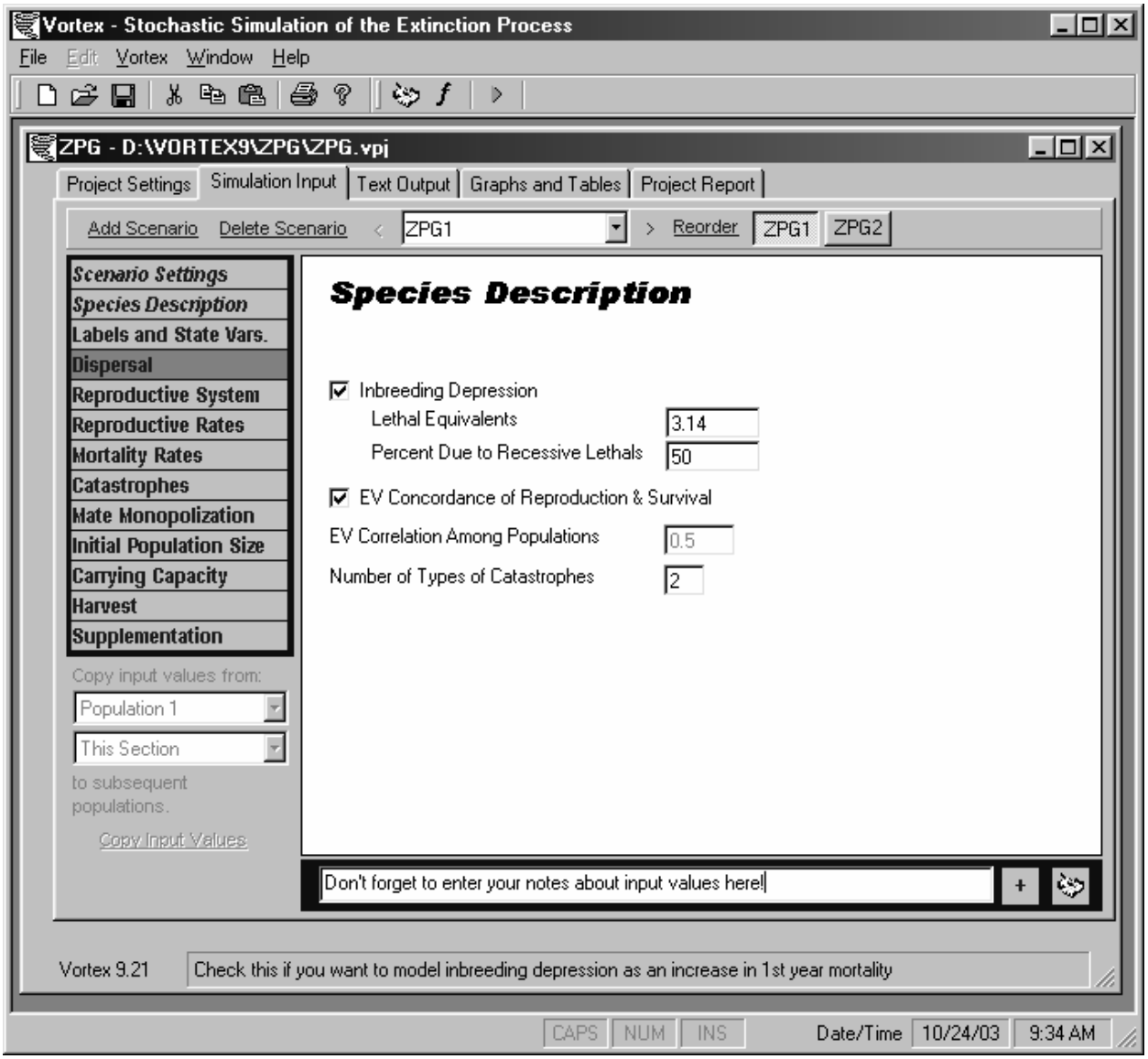


Figure 20. Species Description section of Input.

Inbreeding depression: Check this box if you want to include inbreeding depression in your model, as a reduction in first-year survival among inbred individuals. (See Box B for more information). Although most diploid species that have been studied show depressed fitness when inbred, you may sometimes want to leave inbreeding depression out of your model so that you can compare results with and without inbreeding depression – thereby allowing you to document what impacts inbreeding depression could have on population viability.

Box B: Quantification of Inbreeding Depression

Inbreeding depression is the reduction in fitness commonly observed when individuals are produced by matings between genetic relatives. Inbreeding depression seems to affect most (perhaps even all) species of sexually reproducing organisms, and can cause reduction in survival (of infants, juveniles, and adults), mate acquisition, fertility, fecundity, number of progeny per litter or brood, and a variety of physiological measures related to fitness such as growth rate, disease resistance, stress resistance, metabolic efficiency, sensory acuity, and behavioral dominance (see Lacy 1997 and references therein).

Although inbreeding depression can affect many components of fitness, often the overall effect can be reasonably well summarized by or combined into an effect on infant survival. For example, if inbreeding causes a 10% reduction in litter size, and then a 10% reduction in survival of those individuals born, the cumulative effect would be the same as a 19% reduction in infant survival (resulting in 81% of the yearlings which would have been produced if no inbreeding had occurred). Also, most of the published literature on inbreeding depression in wild species of animals deals only with effects on juvenile survival (Ralls et al. 1988; Lacy et al. 1993). Therefore, the primary way in which inbreeding depression is incorporated into *VORTEX* is through a reduction in first-year survival of inbred individuals. (If desired, inbreeding effects on later survival, reproduction, carrying capacity, and even dispersal can be modeled using functions of inbreeding to specify demographic rates: see Chapter 5 for more information.)

While inbreeding depression is widely known (and has been for centuries), understanding the various possible underlying mechanisms, the ways of quantifying it, and the consequences for population survival and viability is not at all simple. Inbreeding depression may result from recessive deleterious alleles (which are exposed more frequently in homozygous inbred individuals), or from a general disadvantage of homozygotes relative to heterozygotes, or from other genetic mechanisms (see Charlesworth and Charlesworth 1987; Lacy 1993b). In studies of *Drosophila* flies, it has been observed that about half of the effect of inbreeding depression on survival is due to recessive lethal alleles (Simmons and Crow 1977). The relationship between survival and inbreeding caused by the presence of recessive lethal alleles is described by an exponential decline:

$$S = S_0 e^{-bF}$$

in which S_0 is the survival of non-inbred individuals, F is the inbreeding coefficient, b is the average number of lethal alleles per haploid genome (half the number per diploid individual), and S is the resultant survival rate (Morton et al. 1956). Figure B-1 gives the expected relationship between the extent of inbreeding and juvenile survival for a series of hypothetical scenarios differing in the total number of lethal equivalents.

Even if the overall inbreeding depression is due only partly to recessive lethal alleles, the relationship between inbreeding and survival might be expected to be roughly an exponential decline of this form. By observing the relationship between survival and inbreeding, the coefficient b in the above equation can be measured. The value b is a measure of the severity of the effects of inbreeding (not in terms of how inbred the population is—as that is measured by F—but rather in terms of how much fitness is depressed for any given level of inbreeding), and it is the number of recessive lethal alleles per haploid genome that would cause the observed rate of inbreeding depression. This concept is called the number of "lethal equivalents" in the population. A population with 4.0 lethal equivalents per diploid individual (b = 2.0) might have 4 lethal alleles per individual, or it might have 8 alleles per individual which each cause 50% reduction in survival when homozygous, or it might have 2 lethal alleles and four 50% lethals, or any other combination of deleterious alleles which have the same total effect.

VORTEX uses this concept of lethal equivalents to quantify the severity of depression of first-year survival due to inbreeding. Thus, the user must specify how many lethal equivalents characterize the population under study. For only a few species, however, has the number of lethal equivalents been measured in careful breeding studies. Among those species that have been studied, the number of lethal equivalents per diploid ($2b$) ranges from 0 to more than 30, but it is usually in the range of 1 to 5. (Isn't it depressing to know that you probably carry from 1 to 5 alleles which would be fatal

Box B (Continued)...

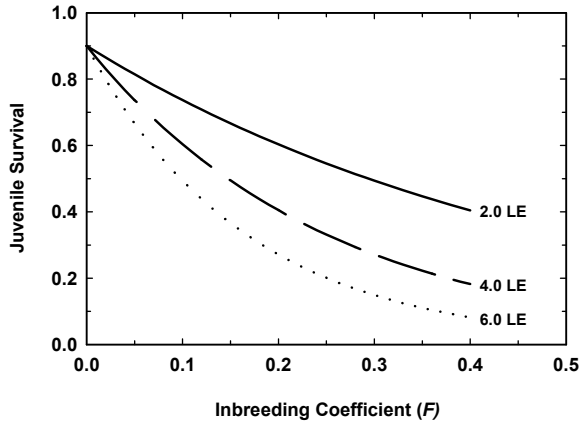


Figure B-1. Expected juvenile survival as a function of inbreeding coefficient under alternative levels of inbreeding depression severity, defined as the number of lethal equivalents (LE) per haploid genome (see text for details).

genetic defects if you had two copies of any one of those alleles? Aren't you glad that you are diploid?) To date, no clear patterns have emerged to suggest that certain taxonomic, ecological, or other categories of species typically have high or low number of lethal equivalents – it seems to be largely a matter of chance whether a population is severely affected by inbreeding or not.

How does VORTEX use "lethal equivalents"?
VORTEX simulates inbreeding depression in two ways, because different genetic mechanisms of inbreeding depression can have different consequences for population viability. Recessive lethal alleles are rather efficiently removed from a population by natural selection when inbreeding occurs. As a result, many individuals may die in the early generations of inbreeding, but when they die they take their lethal alleles with them to the grave, and subsequent generations of individuals have fewer lethal alleles to cause inbreeding depression. (This process is often referred to as "purging the genetic load" of lethal alleles. See Hedrick 1994; Ballou 1997; and Lacy and Ballou 1998.) On the other hand, selection is ineffective at purging inbreeding depression when the inbreeding depression results from a general advantage of heterozygotes over all homozygotes (or, to a lesser extent, when it is caused by recessive sub-lethal alleles).

To model the effects of lethal alleles, which can be removed by selection during generations of inbreeding, *VORTEX* assigns to each individual at the start of a simulation some unique lethal alleles. If inbred descendants happen to receive two copies of the same lethal allele, they are killed. To model the component of inbreeding depression that is not effectively reduced by selection, *VORTEX* calculates the inbreeding coefficient of each individual and then applies an exponential equation like the one above (but using just a part of the total lethal equivalents) to determine how much that individual's survival is reduced. To incorporate these two mechanisms of inbreeding depression, *VORTEX* needs to know (i.e., you need to tell it) how much of the overall inbreeding depression (lethal equivalents) to assign to lethal alleles vs. other genetic mechanisms. As mentioned above, for Drosophila flies, it has been reported that about half of the lethal equivalents are due to actual lethal alleles. Almost no other species have been studied in sufficient detail to quantify the contributions of different types of alleles to inbreeding depression, but the scant data available are not inconsistent with about half of the inbreeding effects being due to lethals in other species as well.

In summary: if you don't know what to enter for inbreeding depression in *VORTEX*, use the default values of 3.14 lethal equivalents (the median of 40 mammalian populations surveyed by Ralls et al. 1988) with 50% of that due to lethal alleles.

VORTEX runs much more slowly when inbreeding depression is included and is modeled with less than 100% of the impact due to lethal recessives (see below). This is because the program will need to calculate and store all pairwise kinships among individuals in the population (N^2 kinships, where N is the maximum population size attained). Therefore, if your population is expected to remain moderately large (perhaps > 250), so that inbreeding will be a rare event, you may want to obtain much greater speed by assuming in your model that inbreeding has no impact on fitness.

VORTEX includes a detailed simulation of genetic change in the populations. At the beginning of a simulation, each founder individual is assigned two unique alleles at each of a number of loci. Each offspring is then randomly assigned one of the two alleles from each parent at each locus. *VORTEX* normally models allele transmission at 5 loci that may contain lethal alleles (allowing up to five unique and independent lethal recessive alleles per founder) and also at one neutral locus (with no impact on inbred progeny). In the Special Options on the Project Settings screen, you have the option of asking *VORTEX* to model alleles at a greater number of neutral loci. Doing so will produce more precise results for genetic trends, and the details of the emergent genetic patterns at the modeled loci can optionally be output to a file for further examination.

In its simplest form, inbreeding depression is modeled in *VORTEX* as a reduction in the survival of offspring during the first year of life. As a result, the program generally underestimates the impact of inbreeding as it can also depress other components of fitness such as adult survival, fecundity, and/or success in competition for mates. (More complex relationships between inbreeding and demographic rates can also be modeled; see Chapter 5 for more on this subject.)

Lethal Equivalents: This box and the next ask you to specify the severity and nature of inbreeding depression in your simulated population. Enter the average impact of inbreeding on first-year survival, quantified as a number of "lethal equivalents" per diploid individual. As described more fully in Box B, the default value of 3.14 is a summary statistic based on a survey of 40 captive mammalian populations (Ralls et al. 1988). If you have specific data indicating a different genetic load, you can enter it here.

Percent Due to Recessive Lethals: Enter here the percent of the total genetic load (quantified by the lethal equivalents you entered into the previous box) that is due to recessive lethal alleles. The number of lethal alleles per founder is limited to 10; therefore, the product of the number of lethal equivalents and the percent of the total genetic load attributable to lethals cannot exceed this number. The lethal alleles are distributed randomly among 10 autosomal loci; thus, the number of lethals per founder will be distributed approximately as a Poisson distribution. A plausible value – one that is consistent with data on *Drosophila* and a few other species that have been studied well – would be 50%. However, cases have been reported in which nearly all of the genetic load is due to lethals, while – in other populations – virtually none of the effects of inbreeding appears consistent with the action of recessive lethal alleles (Lacy et al. 1996). You may wish to test low and high values to see if it affects your simulations of population dynamics. (It probably won't, because it is difficult to maintain a population for long at the very small population sizes at which effective purging of recessive lethal alleles would occur.)

EV Concordance of Reproduction & Survival: Environmental variation (EV) is the annual variation in the probabilities of reproduction and survival that arise from random variation in environmental conditions. (For a more detailed introduction to this topic, refer to Boxes C and D.) EV impacts all individuals in the population simultaneously. The sources of this environmental variation are outside the population; examples include weather, predator and prey population densities, and parasite loads. These factors can affect reproduction and survival independently or simultaneously. Check this box if you think that good years for reproduction are also good years for survival.

Box C: A Brief Statistics Primer

Many demographic characteristics among wildlife species (e.g., birth and death rates, litter size, etc.) fluctuate randomly in magnitude from one year to the next. In order to be able to describe this variability, and to use *VORTEX* most effectively, you must have at least some basic knowledge of a few concepts in statistics.

Population Statistics vs. Sample Statistics
It is important to keep in mind the distinction between the value of a variable or statistic in a population and the value of the variable across a smaller set of observations sampled from that population. Usually, we do not know the true value for the entire population, and that is something we wish to estimate by examining a sample from that population. For some statistics, such as the mean, the best (and unbiased) estimate of the true population value is simply that statistic calculated for the observed sample. For some other statistics, such as the variance and standard deviation, the statistic calculated on the sample is a biased measure of the value for the whole population, so that correction factors must be applied to get a better estimate of the population statistic. Below we somewhat loosely follow a common convention of using Greek letters to symbolize the true (but often unknown) population statistic, Roman letters for sample statistics, and letters with "hats" (for example, $\hat{h}$) to symbolize estimated values.

Measures of Central Tendency and Variability
When a biologist studies a particular demographic characteristic in a wildlife population over some period of time, one generally notes an abundance of values clustered near the middle of a range of annual observations. In the language of statistics, the description of this concentration near the midpoint is a *measure of central tendency*. The most common measure of central tendency is the *arithmetic mean* or, more simply, the *mean*. The mean of a sample of observations is calculated as

$$\overline{X} = \frac{\sum_{i=1}^{n} X_i}{n},$$

which says that the sample mean equals the sum of all measurements in the sample divided by the number of measurements in that sample. Another common measure of central tendency is the median, which is the value at which 50% of the observations fall below and the remainder fall above that value. For a symmetrical distribution, the median will approximate the mean.

To complete our initial description of these data, we must define a *measure of variability* in the data. The most commonly used measure of variability is the *variance*, usually denoted by s^2:

$$s^2 = \frac{\sum (X_i - \overline{X})^2}{n-1}.$$

The "*n*-1" in the denominator is a necessary correction factor to ensure that the estimate from the sample is an unbiased estimate of the variance in the population. (If we measured the variance on the entire population, we would not need this correction and could simply use *n* in the denominator.)

From this equation, it is evident that s^2 gets larger as the amount of variability about the mean increases. The *standard deviation* (*s*), often abbreviated as SD, is the positive square root of the variance and is another very common descriptor of variation in a sample of observations. As you enter data into *VORTEX* for your species, you will be defining the variation in demographic rates in terms of standard deviations. We can also describe variability through the use of the coefficient of variation (here labeled *CV*), in which sample variability is expressed as a percentage of the mean:

$$CV = \frac{s}{\overline{X}} \cdot 100\%.$$

Finally, the simplest measure of variability is the *range* of values observed in the sample. Unfortunately, the observed range is highly sensitive to the number of observations that are made.

Box C (Continued)...

The Binomial Distribution

When summarizing a dataset consisting of a number of individual observations, it is useful to present that summary graphically in the form of a *frequency distribution*, usually in the form of a bar graph. Often we are dealing with data on a dichotomous variable—such as alive or dead, breeding or not breeding, male or female—and we are interested in tallying the frequency of each possibility in a sample of n observations (also known as cases or trials). The probability of any given case belonging to one or the other category is denoted p and q, with $p + q = 1$. The frequency of samples consisting of 0, 1, 2, …, or n observations of a specific category in a sample of n cases is described by a *binomial distribution*. Figure C-1 shows a pair of binomial distributions for $n = 5$.

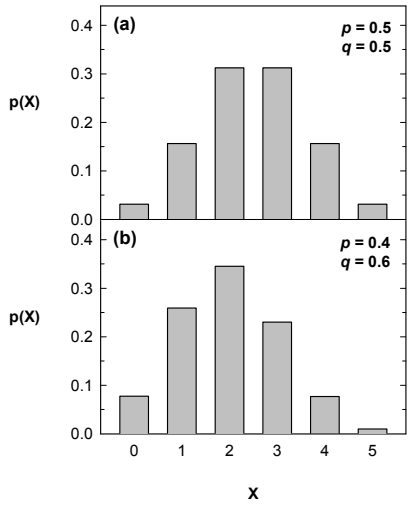


Figure C-1. The binomial distribution for sample size $n = 5$ and (a) $p = q = 0.5$; and (b) $p = 0.4$, $q = 0.6$. The bars give the probabilities $p(X)$ of obtaining a particular number of observations of the first category. For example, with $p = 0.4$ and $q = 1 - p = 0.6$, the probability of obtaining a sample consisting of one observation (out of a possible 5) in the first category is 0.259.

If n observations are sampled from a population with X belonging to one category and $n - X$ in the other, then the population parameter p, the proportion of the observations that is in the first category, can be estimated by the observed proportion within that sample:

$$\hat{p} = \frac{X}{n} .$$

If this sampling procedure were to be repeated a number of times, each estimate of $\hat{p}$ would likely be different. The variance of all possible values of $\hat{p}$ would be

$$\sigma^2_{\hat{p}} = \frac{pq}{n},$$

in which p is the true probability in the population, and q = 1 – p. If p is estimated from the sample, however, then this variance is biased (underestimated); replacing n by $n - 1$ results in a better estimate of the variance of p across samples. The standard deviation of $\hat{p}$ is therefore estimated by

$$s_{\hat{p}} = \sqrt{\frac{\hat{p}\hat{q}}{n-1}}.$$

The Normal Distribution

In a manner similar to the categorical data described by a binomial distribution, continuous variables are generally observed to have an abundance of values nested around the mean with progressively fewer observations near the maximum or minimum values. When these observations are viewed graphically, the resulting frequency distribution takes on the look of the familiar "bell-shaped" curve, particularly when the number of observations (n) becomes large. This curve is more formally described as a *normal distribution*. Figure C-2 shows a typical normal distribution.

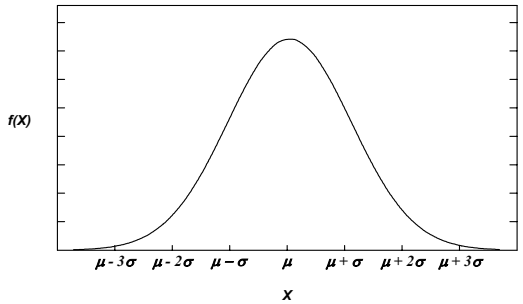


Figure C-2. A normal distribution.

Box C (Continued)...

Note in Figure C-2 the relationship between the population mean (μ) and standard deviation (σ) in a normal distribution. Using a fairly simple method known as *normalizing* a distribution, we can calculate that 68.3% of all observations in a normally-distributed population fall within the range of $\mu \pm \sigma$, 95.5% fall within $\mu \pm 2\sigma$, and 99.7% fall within $\mu \pm 3\sigma$. This kind of information is helpful when estimating standard deviations in demographic rates caused by environmental variation when only a range of observations are available (see Box E for additional details).

It is also noteworthy that the binomial distribution becomes quite close to a normal distribution when the number of observation per sample (n) is large—say, when $n > 20$. Observe that even when n is as small as 5, the distributions shown in Figure C-1 look like approximate bell curves. However, one important distinction between the binomial and normal distributions is the binomial distributions are always bounded at 0 and n, while normal distributions have "tails" that are infinitely long, but rapidly diminishing.

For more information on the theory and applications of these and many other concepts relevant to an understanding of population dynamics and risk projections, see Caughley (1977), Sokal and Rohlf (1994), and Zar (1996).

Case Study II:
Correlating environmental variation for reproduction and survival

North America's whooping crane (*Grus americana*) shows a classic migratory pattern typical of many bird species. The last remaining substantial population breeds in Alberta's Wood Buffalo National Park and spends the winter at Aransas National Wildlife Refuge along the Gulf Coast of Texas. Because of this movement pattern, the environmental conditions affecting chick production are quite different from those impacting mortality during the majority of the year (Mirande et al. 1991). Consequently, we would expect EV affecting these processes to be uncorrelated when constructing a *VORTEX* model

EV Correlation Among Populations: You specify here the correlation of EV among populations (applicable, of course, only when more than one population is modeled). If this value is set to 0.0, then EV will be completely independent among populations. If this value is set to 1.0, then EV in reproduction and in survival will be completely synchronized among populations. As a result, good years for reproduction and / or survival in one population will lead to similarly good years in all other populations. If this degree of correlation is set to an intermediate value, then EV will be partly correlated among populations.

Environmental variation in the metapopulation context can be considered to exist at two levels: local (population-specific) and global (acting across all populations). The total EV, when expressed as a variance rather than a standard deviation as entered by the user, is simply the sum of the EV existing at these two levels. The correlation of EV among populations that you enter, then, is simply the proportion of the total EV (when expressed as a variance) that is global in scope (i.e., common to all populations).

Box D: The Statistics of Demographic Stochasticity and Environmental Variability

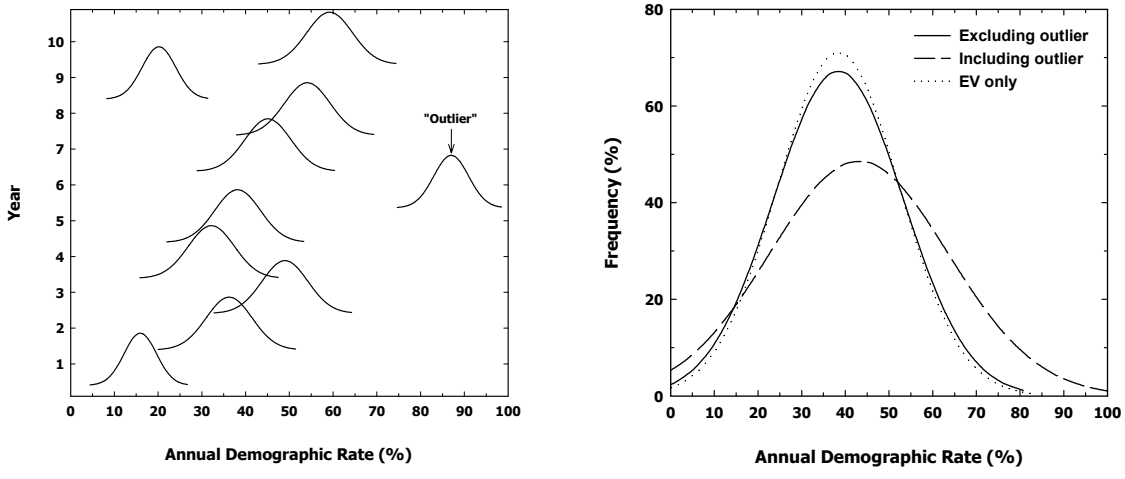
Now that you have reviewed some of the general definitions of central tendency and variability (see Box C), as well as some characteristics of the binomial and normal distributions, we can discuss the statistical nature of demographic and environmental stochasticity.

Demographic stochasticity is the random fluctuation in observed birth rate, death rate, and sex ratio of a population resulting from stochastic sampling processes, even if the probabilities of birth and death remain constant over time. In such cases, the annual variation in numbers of individuals that are born, that die, and that are of a given sex can be specified from statistical theory and would be expected to follow binomial distributions. *Environmental variability* is the annual fluctuation in probabilities of birth and death arising from random fluctuations in the environment (e.g., weather, abundance of prey or predators, prevalence of nest sites, etc.). Annual fluctuations in the probabilities of reproduction and mortality are modeled in *VORTEX* as binomial distributions, while environmental variation in carrying capacity (see Box F for more on this topic) is modeled as a normal distribution.

Note that the distinction between demographic stochasticity and environmental variability is a subtle one (even some professional population biologists have been confused by this!). Demographic stochasticity is the variation in an observed vital rate due to the sampling variation that is inherent because each individual (an observation) is an independent and random sample from a population with a given mean or probability. Hence, it is the variation in sample means ($\bar{X}$) around a fixed population mean (μ). Environmental variation, on the other hand, is variation (due to extrinsic factors that vary over time) in the population mean itself (i.e., μ is different each year).

Putting this information together, we conclude that the variation across years in the frequencies of births and deaths—both in real populations and our simulated *VORTEX* populations—will have two components: the demographic variation resulting from binomial sampling around the mean for each year, and additional fluctuations due to environmental variability. In actuality, catastrophic events (to be discussed in more detail later in the *User's Manual*) also contribute to the overall observed variation across many years of data, but they are treated separately from standard annual environmental variability.

Figure D-1. *Left panel:* Expected values for a given annual demographic rate, showing binomial sampling variance arising from demographic stochasticity with a sample size (n) of 100 individuals. *Right panel:* Frequency distribution of that same demographic rate based on observed mean and variance of annual values. Solid and dashed curves show the normal distributions that most closely fit the observed data with and without the catastrophic "outlier", while the dotted line shows the normal approximation to the binomial distribution expected solely from environmental variability (and excluding the outlier). The difference between the solid and dotted lines gives the variation attributable to demographic stochasticity.



Box D (Continued)...

The left panel of Figure D-1 shows ten years of expected values of a given demographic rate—say, juvenile mortality—in a simulated wildlife population. Each "bell-shaped" curve depicts the probability distribution we would expect from demographic stochasticity acting on that rate in that year (Actually, these little curves of demographic stochasticity would be binomial, but the normal distributions are close enough for illustration purposes). For example, the expected rate (μ) in year 1 is 15.2%. However, when the fate of each juvenile in the population is considered, it is possible that the actual rate may deviate from 15.2% solely from this sampling process. In addition, the expected mortality changes from year to year due to environmental variation, with each annual curve again reflecting the sampling variance (demographic stochasticity) expected for that year's value. Note that these curves become tighter (the standard deviation resulting from demographic stochasticity decreases) as the means deviate from near 50%. In addition, notice that the mortality rate in year 7 is particularly high; perhaps a catastrophic event occurred in that year to produce such high mortality.

With annual rate data in hand, we can actually calculate the relative contributions that demographic stochasticity (DS) and environmental variability (EV) make to the total observed variance. Consider the example presented in Figure D-1. The mean mortality rate calculated from these annual data is 0.387 with a standard deviation (combining effects of DS and EV) of 0.148. Note, however, that the catastrophe shown as the outlier in the dataset was not included in this calculation; if it were, the mean and standard deviation would change to 0.435 and 0.204, respectively. If we consider the data with the outlier absent, we can calculate the standard deviation due to EV:

$$\sigma_{EV} = \sqrt{\sigma^2_{EV}} = \sqrt{\sigma^2_{TOT} - \overline{\sigma^2_{DS}}}$$

where σ^2_{TOT} is the total variance across the data and $\overline{\sigma^2_{DS}}$ is the mean sampling (binomial) variance across the individual rates (see Box B for how to calculate a binomial variance). In the example above, the mean binomial variance turns out to 0.0022. Therefore,

$$\sigma_{EV} = \sqrt{\sigma^2_{EV}} = \sqrt{0.0219 - 0.0022}$$
$$= 0.140$$

which is the variation across years of the mean (peak) values for each curve in the left panel of the figure. This calculation tells us that the contribution of demographic stochasticity to the total variance observed in our nine years of mortality data (remember, we removed the outlier from the analysis) is quite small—the variance attributable to environmental variability is almost 90% of the total variance in mortality. This is shown graphically in the right panel of Figure D-1. In order for demographic stochasticity to make a significant contribution to the total observed variance, the number of individuals sampled for a given rate (*n*) would have to be quite small—on the order of a few tens.

The right panel of Figure D-1 also shows the frequency distribution obtained by including the catastrophe outlier in the calculation of overall mean and variance. The inclusion of this single observation results in a significantly poorer fit to the data, as the overall distribution of values (the mean of all values in the left panel) does not look much like a normal distribution. This helps in part to illustrate why catastrophes—events that are infrequent in occurrence yet severe in population impact—are treated separately from more typical annual or seasonal fluctuations.

Finally, it is instructive to note that each of the distributions in the right panel of Figure D-1 extend beyond 0.0 and/or 1.0. As this is biologically implausible, we need to truncate these distributions in order to allow their proper use in defining probabilities. Partly for this reason, *VORTEX* usually uses a binomial distribution (which does not extend beyond 0% and 100%, but which otherwise looks much like a normal distribution) to represent EV. For ease of calculation, *VORTEX* sometimes does use a normal distribution when it is a very close approximation to the binomial, but it then truncates the normal curve symmetrically about the mean to avoid creating any bias.

Box D (Continued)...

The above methods are a bit complex. Because DS is usually quite small when the sample sizes (*n*) are at all large, a quick, somewhat generous, estimate of EV is simply the total variation in rates observed across years (treating DS as an insignificant contributor to the observed variation).

Finally, keep in mind that the *VORTEX* simulation program generates DS automatically as it determines whether each individual lives, whether it breeds, and what sex it is. Unlike some other PVA programs, you do not specify that DS should be added into the model, and you cannot exclude it (from the model or from real life). You do need to specify the magnitude of EV, however, as EV results from external processes rather than being an intrinsic and inevitable part of all population dynamics. The size of DS is a consequence of the population size; the size of EV depends on the constancy of the environment.

Number of Types of Catastrophes: Catastrophes can be thought of as extremes of environmental variation that strongly impact reproduction and/or survival. Types of catastrophes might include sudden habitat destruction, floods, forest fire, epidemic disease outbreaks, etc. Catastrophes can be significant threats to small, isolated populations. For example, disease decimated the last population of black-footed ferrets, and a hurricane killed half of remaining wild Puerto Rican parrots. It is up to you to determine what types of catastrophe, if any, may impact your population. Later in the data input process, you will be given the opportunity to define how each type of catastrophe will impact reproduction and survival.

You may be able to identify historical catastrophes by examining birth and/or death rate data over several past years for your species of interest. If you find a demographic rate that is significantly different than that described by normal levels of variation—for example, at least 2 standard deviations from the mean value—you may use that as evidence of a catastrophic event.

Dispersal Among Populations

If you are modeling a metapopulation, you now need to specify a few parameters that help to define the system of dispersal of individuals among populations. In a later section you will define the rates of dispersal of individuals between populations.

Age Range – Youngest and Oldest: In these boxes, enter the youngest and oldest ages of those individuals that move between populations. If both sexes are capable of moving between populations, and the ages at which males and females disperse are different, you must decide which age(s) you use for these fields. This decision will be based largely upon how conservative you want to be about your estimation of potential risk. For example, if males begin moving among populations at 3 years of age and females at 5 years of age, entering **3** as the youngest age to disperse may underestimate the risk of population decline and/or extinction since females are allowed to move at an earlier age in the model.

Dispersing Sex(es): Check the appropriate box(es) to specify whether males, females, or both can disperse from the natal population.

Percent Survival of Dispersers: Often, dispersal among populations occupying discrete areas of suitable habitat is dangerous. Traversing the matrix of unsuitable habitat between populations may expose an individual to additional risks of predation or lack of food, and entry into a new population may require competition with the established residents. Enter here the survival rate (as a percent) of individuals that are dispersing between populations. The dispersal mortality is imposed separately from other mortality detailed elsewhere in the program. (More specifically, this dispersal mortality is imposed after annual mortality. See Appendix IV for a detailed description of *VORTEX* program flow.) A dispersal survival rate

of 80% means that there is a 20% chance that an individual will die during the process of moving from population A to population B.

Dispersal Modifier Function: Dispersal patterns can be very complex and determined by many factors. *VORTEX* does not provide a full model of dispersal across complex landscapes, but instead models movements among discrete populations, with the user specifying the rate of movement between each pair of populations (as you will do in a later Input section). However, this box provides you with the opportunity to customize dispersal, in perhaps very complex ways. Any function entered here will be used as a modifier of the rates to be entered later. For example, you could cause dispersal of males to be twice as high as the specified rate (and twice as high as for females), by entering "=D*(1+(S='M'))". The parameter 'D' in the equation stands for the specified dispersal rate between any two populations. Such dispersal modifier functions can be used to cause dispersal to be dependent on sex, age, inbreeding, population density, and many other characteristics of the individuals and populations.

With respect to dispersal or other aspects of population dynamics, the standard *VORTEX* model may not match precisely the behavior of your species. Often, the differences between the model and reality will not cause substantial differences in long-term population dynamics and risk. (Although definitive confirmation of this assumption may require testing a more complex and complete model to see if the refinements do matter.) In many cases, *VORTEX* does provide the capability to create models that are more complex – sometimes much more complex! – than the standard *VORTEX* model. These more complex population models are built by using functions rather than constants for input values. Using such functions provides considerable flexibility, but you should use them cautiously if you are not yet fully familiar with the *VORTEX* model.

When you are finished with entering Species Description parameters, click on the heading for Labels and State Variables on the left-hand list.

Labels and State Variables

In this Input section, you can enter optional labels for your populations, as well as define parameters that describe characteristics or "states" of your populations and individuals.

Population Labels and State Variables: *VORTEX* allows the user to enter a label for each population being modeled (Figure 21). The labels can be any text, up to 20 characters long. These population labels will be used as headers for entry of population-specific demographic rates (on subsequent data entry screens) and as labels in the output files. One population label is entered per line.

When entering a population label, the user may also specify up to two numbers for use as "state variables" describing some characteristic of the population. These state variables must be numeric values that are entered on the same line as the population label. State variables may describe characteristics such as measures of habitat quality or habitat suitability for the population, elevation or some other descriptor of the habitat, or perhaps an identifying code for the subspecies or local population. This option of entering population state variables is provided so that demographic rates (such as fecundity, mortality, and carrying capacity) can be specified to be functions of these state variables. (See Chapter 5 for a description of the use of functions for demographic rates.) In such functions, the state variables are symbolized (in order) as **B** and **C**. (Symbol **A** is used for age.) Functions characterizing the demographic rates for each population could always be entered in earlier versions of *VORTEX* even without using state variables, but the use of state variables can allow for a more consistent representation of demographic rates across populations and easier testing of the effects of varying habitat or population characteristics. These capabilities will be explained in much greater detail in Chapter 5.

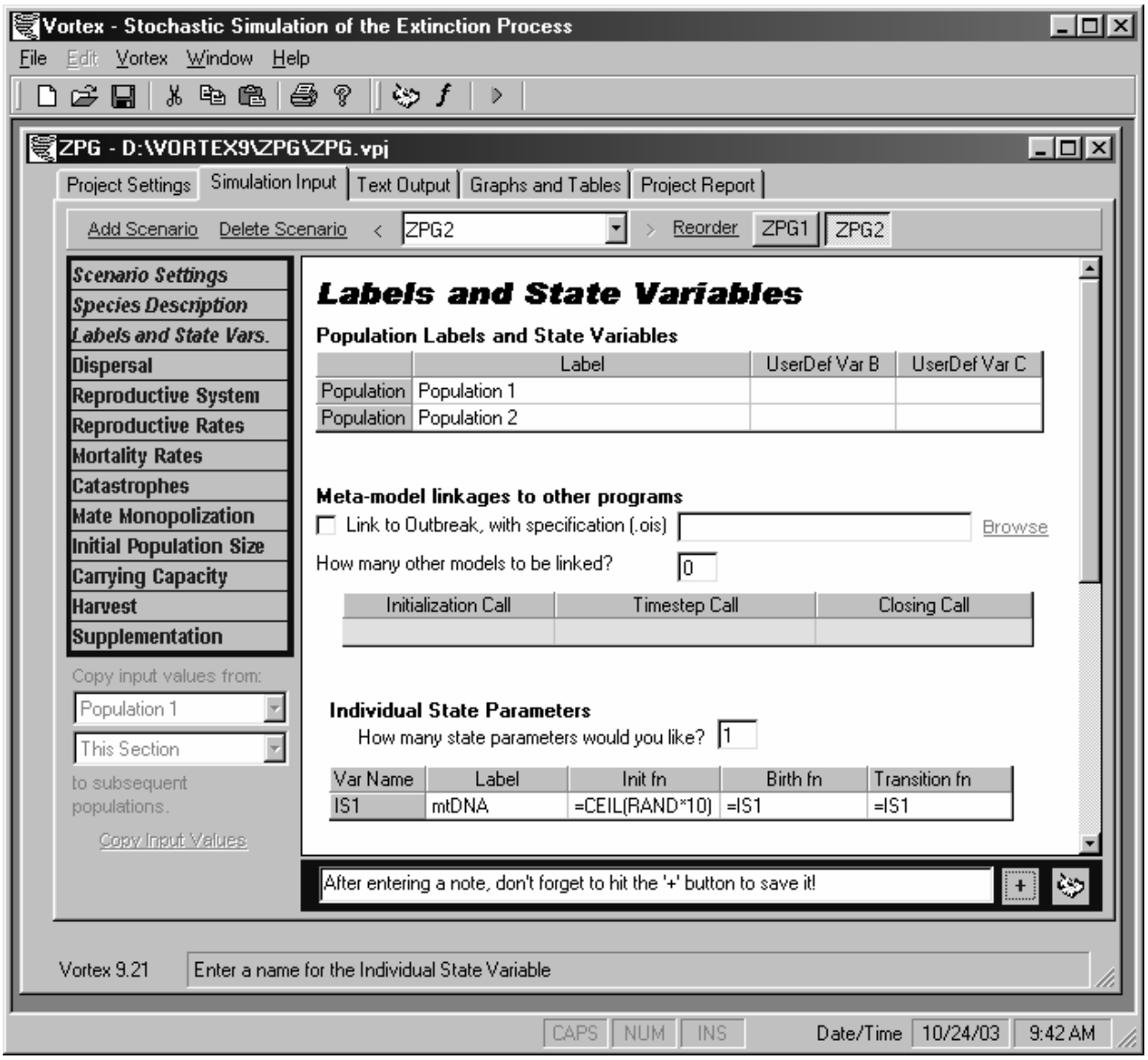


Figure 21. Labels and State Variables Input section.

Meta-model linkages to other programs: VORTEX provides the capacity to run the population simulation simultaneously (functionally in parallel) with one or more other models that might describe the dynamics of parts of an overall system. For example, an epidemiological modeling program, *OUTBREAK,* can model the dynamics of an infectious disease in the population. *VORTEX* and *OUTBREAK* can be run at the same time on the same simulated population, with *VORTEX* simulating demographic and genetic changes and constantly informing *OUTBREAK* of the current census of the population, while *OUTBREAK* models the changes of disease state (susceptible, latent infected, infectious, recovered) and constantly informs *VORTEX* which individuals are in each state. The disease states can then be used to modify reproduction, survival, dispersal or other demographic rates for individuals in the meta-model. More information about *OUTBREAK* will be made available at http://www.vortex9.org/outbreak.html.

At this time, *OUTBREAK* is the only other model that is provided for linking with Vortex. In the future, we plan to provide also built-in links to GIS models of landscape change, models of animal movements on the landscape, and perhaps other models. However, *VORTEX* already provides the capability for a user to

create (or otherwise obtain) his or her own model and link it to *VORTEX* as a dynamic, multi-component meta-model. This capability of *VORTEX* to link with other models is still being developed and tested. Full explanation of the proper use of meta-models is beyond the scope of this manual, and *users are strongly cautioned to not expect to be able to build and use meta-models without the assistance of an expert*. Lacy and Miller (2002) discuss the conceptual need to link PVA models with other kinds of knowledge.

Individual State (IS) Parameters: VORTEX provides the user with the option of creating up to nine "Individual State" parameters that define characteristics of individuals. These state parameters may represent any feature of the organism that can be specified or coded by a numeric value. For example, dominance status might be encoded as Dominant = 1.0; Subdominant = 2.0; and Subordinate = 3.0. Or a state variable might be used to represent some measure of body condition. Or two state variables might be used to track the x and y coordinates of each individual's location on a landscape.

To create one or more individual state variables, check the box, then indicate how many variables you will be creating. For each variable, you then enter into the table a label, which can be any text that will help you to remember what parameter you were representing. The *VORTEX* program, however, will track the Individual State variables with the labels IS1, IS2, etc., as indicated in the first column of the table.

For each IS variable, you need to enter three functions (or constants) to define: (a) an initialization function (Init fn) – the starting value for each individual at the beginning of the simulation; (b) a birth function (Birth fn) – the value for each newborn individual; and (c) a transition function (Transition fn) – the change in state (if any) each year of the simulation. These functions are entered in the same way as other functions that can be used to specify demographic rates (see Chapter 5).

Case III:
Using an Individual State Variable to model transmission of mitochondrial DNA haplotypes

Mitochondrial DNA haplotypes are inherited from the maternal parent. This matrilineal transmission can be modeled by creating an Individual State Variable (IS1, labeled "mtDNA"). To assign randomly one of 10 haplotypes (encoded 1 through 10) to the founder individuals, specify a Initialization Function of "=CEIL(RAND*10)". The maternal inheritance is defined simply with the birth function of "=IS1", because the individual state parameters for use in the birth function are set at birth to be the values from the maternal parent (pending redefinition in the birth function). In the absence of mutation, the transition function also would be "=IS1", to preserve the value for each individual across years. To model mutation to one of the original haplotypes, with mutation rate 0.0001, the transition function could be set to "=(RAND< 0.00011)*(CEIL(RAND*10))". The mutation rate used in the function has to be elevated by 10% to account for the cases in which mutation would be to the existing haplotype, leaving the value unchanged.

Once the mtDNA haplotype is defined as an individual state variable, demographic rates can be specified to be functions of an individual's haplotype. The final frequencies of haplotype will not be tallied by *VORTEX* (because *VORTEX* doesn't even know that the Individual State Variable you created is a categorical variable). However, you can obtain a complete listing of all individuals at the end of the simulation, including their state variables, by selecting the Special Option (from the Project Settings screen) to "Produce a file of all living individuals at the end of each iteration." You can then analyze those data in whatever spreadsheet or other utility software you prefer.

Dispersal Rates

This next section of input (Figure 22) is accessible only if you specified (in the Scenario Settings) that your scenario is to have more than one population. In the grid on this screen, you enter dispersal rates to specify the probability that a given individual of the appropriate age-sex class will disperse from population A to population B in a specific year. That is, a rate of 1.00 indicates a 1% probability that an individual will migrate from population A to population B. Equivalently, if a population consists of 100 one-year old females with a dispersal rate between two populations of 1%, then one of these females would, on average, be expected to disperse in that direction in any given simulation year.

Dispersal rates need not be symmetric among populations; enter whatever probability you deem appropriate for each pair of populations. Enter **0** to indicate no exchange of individuals between a pair of populations. The values on the diagonal of the grid – the percents of individuals that do not disperse each year – is automatically calculated by the program so that the rows will sum to 100%.

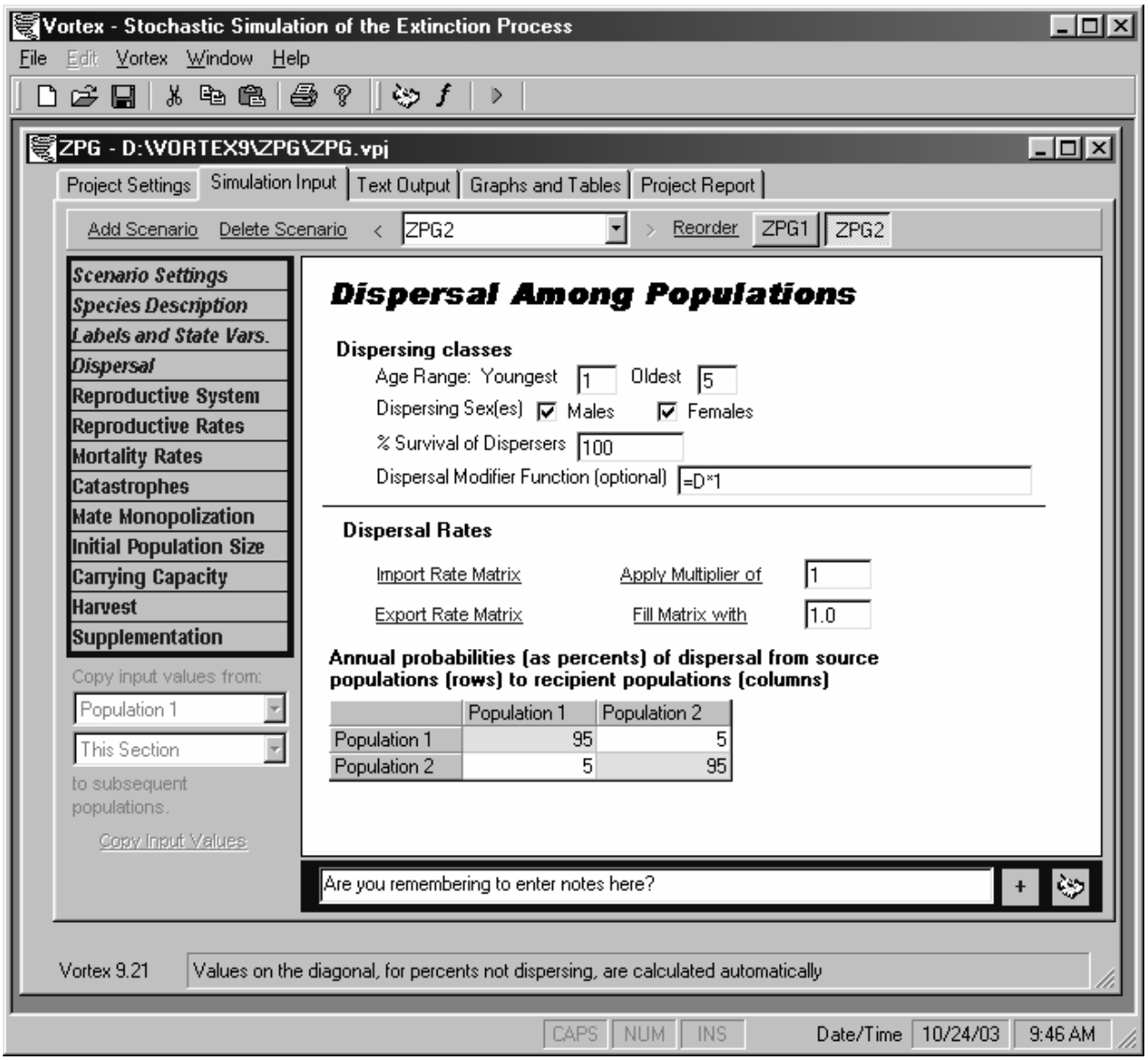


Figure 22. Dipersal Rates input section.

It is important to remember that while most input data should be in the form of percentages, a few others are input as proportions. Check the labels and prompts for clarification of the required data format.

On the Dispersal Rates screen are five commands that can make it easier to enter dispersal rates. "Import Rate Matrix" allows you import the grid values from a semi-colon delimited text file. This file can be created in Excel or whatever software you choose. It must contain values for all cells of the grid, including the labels (although the labels in the file will be ignored and will not over-write what shows on the screen). The easiest way to see the format of the rate matrix file is to select "Export Rate Matrix", and then look at the file that was created. With these commands, you can create a large matrix in a spreadsheet program, and then import it into *VORTEX*, and you can export rate matrices for modification or for re-use in other *VORTEX* projects. When you have only a few populations, these commands are usually not worth using. However, if you have, for example, 40 populations, you very well may want to use Excel to generate your dispersal rate matrix rather than typing in all 1560 pairwise dispersal rates!

The commands to "Make Cells Square" and "Make Cells Original Shape" are simply there to help you show the grid in a format that is easier for you to view. The fifth command available allows you to apply a multiplier to each non-diagonal cell in the grid. By entering a value and hitting "Apply Multiplier of " you can shift all of the dispersal rates upwards or downwards. This makes it much easier to test a range of dispersal rates across Scenarios of your Project. For example, you might enter an initial set of rates, and then apply multipliers of 0, 2, and 4 in order to test no dispersal, and 2x, and 4x increases in dispersal.

VORTEX provides you with significant flexibility in defining dispersal rates for individuals within a metapopulation. That is, rates may be inversely proportional to distance, directly proportional to habitat area, or they may be defined through a more complex determining function. However, you have the task of calculating these rates for each pair of populations—*VORTEX* does not calculate them for you based on a set of internal rules. A considerable body of literature exists on the methods for estimating dispersal rates between populations. Capture-recapture studies can provide some of the best data for this process of estimation, although experimental difficulties do exist (see Ims and Yoccoz (1997) for more information). An example of estimating dispersal rates from molecular data is described in Case Study IV.

Case Study IV:
Estimating migration rates from DNA sequence data

The Anacapa Island deer mouse (*Peromyscus maniculatus anacapae*) is endemic to the Anacapa islands off the coast of California near Los Angeles. Pergams et al. (1999) conducted a population viability analysis to develop a comprehensive management plan involving the potential for captive breeding, reintroduction, or translocation of individuals following eradication of introduced rats.

Nucleotide sequences were obtained from the mitochondrial DNA (mtDNA) cytochrome oxidase subunit II gene of mice sampled across each of the three Anacapa Islands. Based on the average amount of nucleotide sequence divergence among mice from the different islands, the authors were able to directly calculate an estimate of gene flow, *Nm*, where *N* is the average size of a pair of islands and *m* is the average rate of migration between those islands per generation (see Nei 1982 for details). For example, *Nm* between Middle and West Anacapa was calculated to be 7.27 individuals per generation. Since a generation in Anacapa Island deer mice is only 84 days, and assuming a time cycle of 21 days for the analysis, the number of individuals migrating between the two islands is (7.27)(0.25) = 1.8175 per time cycle. The average population size across Middle and West Anacapa Islands was estimated to be 19,044 mice, so the migration rate is then calculated to be 1.8175/19,044 = 0.0000954. Finally, the authors assumed a symmetrical pattern of migration, so that the estimate of the rate of migratin from Middle to West Anacapa (equivalent to that from West to Middle Anacapa) is (0.5)(0.0000954) = 0.0000477.

Reproductive System

Monogamous, Polygamous, Long-term Monogamy, or Long-term Polygamy: *VORTEX* models breeding systems as monogamous vs. polygamous, and short-term vs. long-term. With monogamous breeding, there must be a male for every breeding female; males may therefore become a limiting factor restricting breeding. In polygamous models, there only needs to be at least one male for all females to have an opportunity to breed. However, in a later section (Mate Monopolization) you can specify that only a subset of males have opportunities to breed. For example, you can create a polygynous system in which some males control harems of typically 5 females, while the remaining males are excluded from breeding.

If you do not choose a "Long-term" option, then *VORTEX* will assume that mates are randomly reshuffled each year and that all available individuals have an equal probability of breeding. If you do specify one of the "Long-term" models, then once pairs are formed, those pairs will remain together across years of the simulation until either the male or the female dies or disperses to a different population. Demographically, it will not matter whether you choose long-term pairings or re-arrangement of pairs each year. Genetically, there may be a small effect on the rate of loss of genetic diversity from the population.

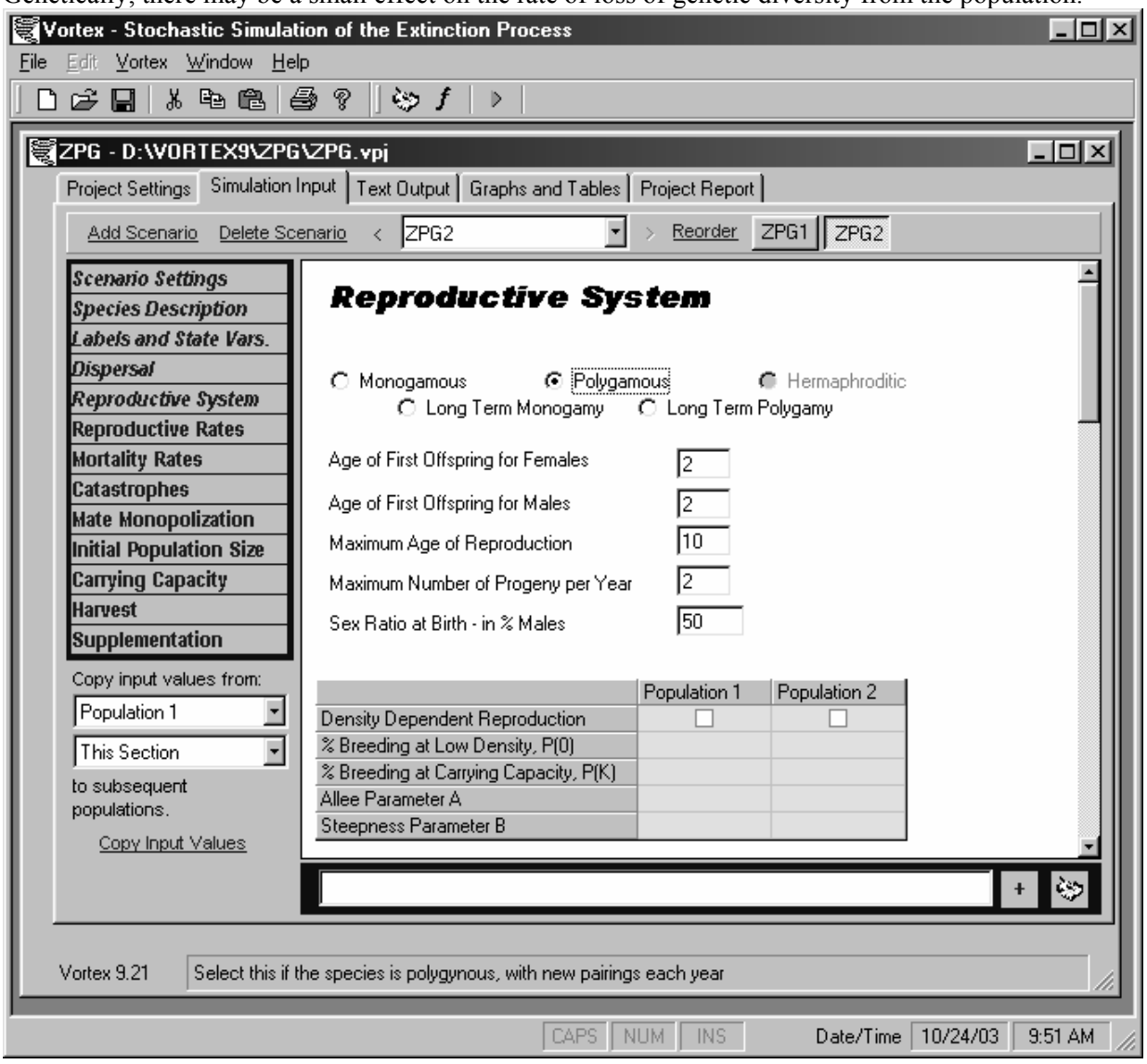


Figure 23. Reproductive System input section.

VORTEX does not fully customize the details of mating systems because of the complexities of considering a wide variety of species and their particular characteristics. More complex breeding systems can substantially impact genetic variation, but are less likely to seriously alter the demographic performance of a population. In the future, *VORTEX* will also allow you to model a species with hermaphroditic breeding—that is, a species in which each individual is both male and female and can therefore potentially mate with any other individual, including itself. Presently, this option is not yet enabled.

Age of First Reproduction for Females (and Males): VORTEX defines breeding as the time when the first offspring are born, not the age of onset of sexual maturity or the age of first conception. The program also assumes that breeding (and, for that matter, all other events) occurs at discrete intervals—usually years, but this can be described in terms of whatever you have defined as a suitable time cycle. Thus, breeding age must be entered as an integer value; you cannot enter **2.5** years as the first age of breeding but must enter either **2** or **3** years. In addition, you should enter the median age of first breeding, not the earliest age ever observed since the earliest observed age may not be typical of the normal population behavior.

Case Study V:
Estimating age of first breeding in males and females

The babirusa (*Babyrousa babyrussa*) is one of the more interesting endemic mammals on the Indonesian island of Sulawesi. Individuals in captivity can reach sexual maturity as early as 5 months of age. However, most captive animals approach the age of one year before reaching sexual maturity. Even at this age, the animals are quite small and it is considered unlikely that they will reproduce until they are older than one year of age. Taking into account the gestation length of about 5 months (usually 155 – 158 days), it is likely that female babirusa in the wild will have their first litter at the age of 2 years. On the other hand, males of this age will have to deal with strong competetion for mates among older and stronger males. Consequently, Manansang et al. (1996) developed *VORTEX* models for this species in which the age of first breeding among males was estimated to be delayed until 4 years.

Maximum Age of Reproduction: VORTEX assumes that individuals can breed at a rate typical for that species throughout their adult lifespan. If your species does not reproduce throughout its entire adult life, do not enter the species' maximum life expectancy. For example, humans typically reach reproductive senescence before they die. In this case, if the typical life expectancy is 70 years but they cease reproduction at 50 years, then enter **50** as the maximum breeding age.

Maximum Number of Progeny per Year: Enter the most individuals born to a given female during a year (time cycle). If your species produces more than one set of offspring (in the form of litters, clutches, pods, etc.) per year, but you are using a year as your time cycle, add each set together and then enter the total number born during the year. You can enter the maximum number that has ever been recorded—even though such an event may be quite rare—and later on during the data input process you can then assign a low probability of occurrence to this maximum value.

You have the option of entering a mean and standard deviation for the distribution of offspring numbers, rather than specifying the percentage of females producing each possible number of young (see below). This removes the limitation on the size of offspring numbers that can be modeled, and therefore makes it much easier to model species with high fecundities. To choose this option, enter **0** for the maximum number. Subsequent screens will allow you to specify the nature of this normal distribution (see p. 51).

When annual offspring numbers per female are not large—for example, on the order of five or fewer—it is recommended to specify the exact distribution, rather than using the optional normal distribution.

Case Study VI:
Modeling species with high fecundity

The distribution of the winged mapleleaf mussel (*Quadrula fragosa*) has been reduced to only a few sites in the St. Croix River between Minnesota and Wisconsin in the United States. As is typical of nearly all freshwater bivalves, this species reproduces by broadcasting a large number of larval offspring known as glochidia into the water column. Kjos et al. (1998) estimated that an adult female mussel produced a mean number of 171,000 glochidia in a typical breeding cycle. Only those glochidia that locate and encyst within the gills of its host fish, excyst following metamorphosis, and then settle onto suitable substrate on the river bottom will survive to the subadult age class.

Because of the impossibility (at least with today's computer systems) of tracking such a large number of individual offspring, *VORTEX* cannot normally deal with such high levels of fecundity. However, this situation can be made much more tractable by simply redefining what is meant by "reproduction"; instead of defining it in terms of the production of glochidia, we can define it as the number of individuals that successfully settle onto suitable river-bottom substrate. Kjos et al. (1998) estimated that only about 0.2% of the glochidia find and successfully encyst onto a host, that about 15% of those successfully metamorphose and excyst, and about 20% of those excysted juveniles settle onto suitable substrate. In other words,

Final brood size = [171,000 glochidia]×[0.002 encyst]×[0.15 excyst]×[0.2 settle] = 10

By condensing a series of mortality events from the very early stages of the mussel's life cycle, the authors were able to define a system of reproduction that was amenable to the *VORTEX* modeling system. Other types of organisms that would benefit from this type of simplification include amphibians, fish, and even insects.

Sex Ratio at Birth: Enter here a number between 0.0 and 100.0 to represent the average percentage of newborn offspring that are male. This number is typically very near 50%, signifying a roughly equal male:female sex ratio at birth. If relatively more or fewer males are born to a given female per year, enter the appropriate percentage (e.g., **55** for 55% males).

Density Dependent Reproduction: Does the reproductive rate of your species change with changing population size? That is, is reproduction low when the population is small due to a difficulty in finding mates or, conversely, does reproduction drop off when the population is large (more specifically, at high density) due to limited resources or territories, intraspecific competition, crowding, stress, etc.? If so, check the box and then enter the subsequent parameters defining the nature of the density dependence.

If your population's reproduction is density dependent, you will need to model this relationship. *VORTEX* models density dependence with an equation that specifies the proportion of adult females that reproduce as a function of the total population size. Normally, the proportion of females breeding would decrease as the population size becomes large. In addition, it is possible to model an Allee effect—a decrease in the proportion of females breeding at low densities due, for example, to difficulty in finding mates. The equation that *VORTEX* uses to model density dependence is:

$$P(N) = (P(0) - [(P(0) - P(K))\left(\frac{N}{K}\right)^{B}])\frac{N}{N + A}$$

in which $P(N)$ is the percent of females the breed when the population size is N, $P(K)$ is the percent that breed when the population is at carrying capacity (K, to be entered later), and $P(0)$ is the percent of females breeding when the population is close to zero (in the absence of any Allee effect). The exponent B can be any positive number and determines the shape of the curve relating the percent breeding to population size, as the population becomes large. If $B = 1$, the percent breeding changes linearly with population size. If $B = 2$, $P(N)$ is a quadratic function of N. Figure 24A shows representative density-dependence curves for different values of B in the absence of an Allee effect.

The term A in the density dependence equation defines the magnitude of the Allee effect. One can think of A as the population size at which the percent of females breeding falls to 50% of its value in the absence of the effect (Akçakaya 1997). Figure 24B shows several density-dependence curves for different values of A with a steep decrease in breeding at high densities ($B = 8$). Figure 24C gives the same curves as in Figure 24A, but with the addition of an Allee effect ($A = 1$).

By inspecting the density-dependence equation, one can see that when the population is at carrying capacity, $P(N) = P(K)$. When the population is very small (N is near 0), then $P(N) = P(0)$ if there is no Allee effect. It is also apparent that the Allee effect term $[N / (N + A)]$ will have a strong impact on the value of $P(N)$ when N is small. When N is much larger than A, the Allee term will have very little effect on the value of $P(N)$. Fowler (1981) provides a review of density-dependence functions and presents some density curves for large mammals. We have chosen to model density dependence using the equation given above because it provides the user with considerable flexibility—despite its relatively simple

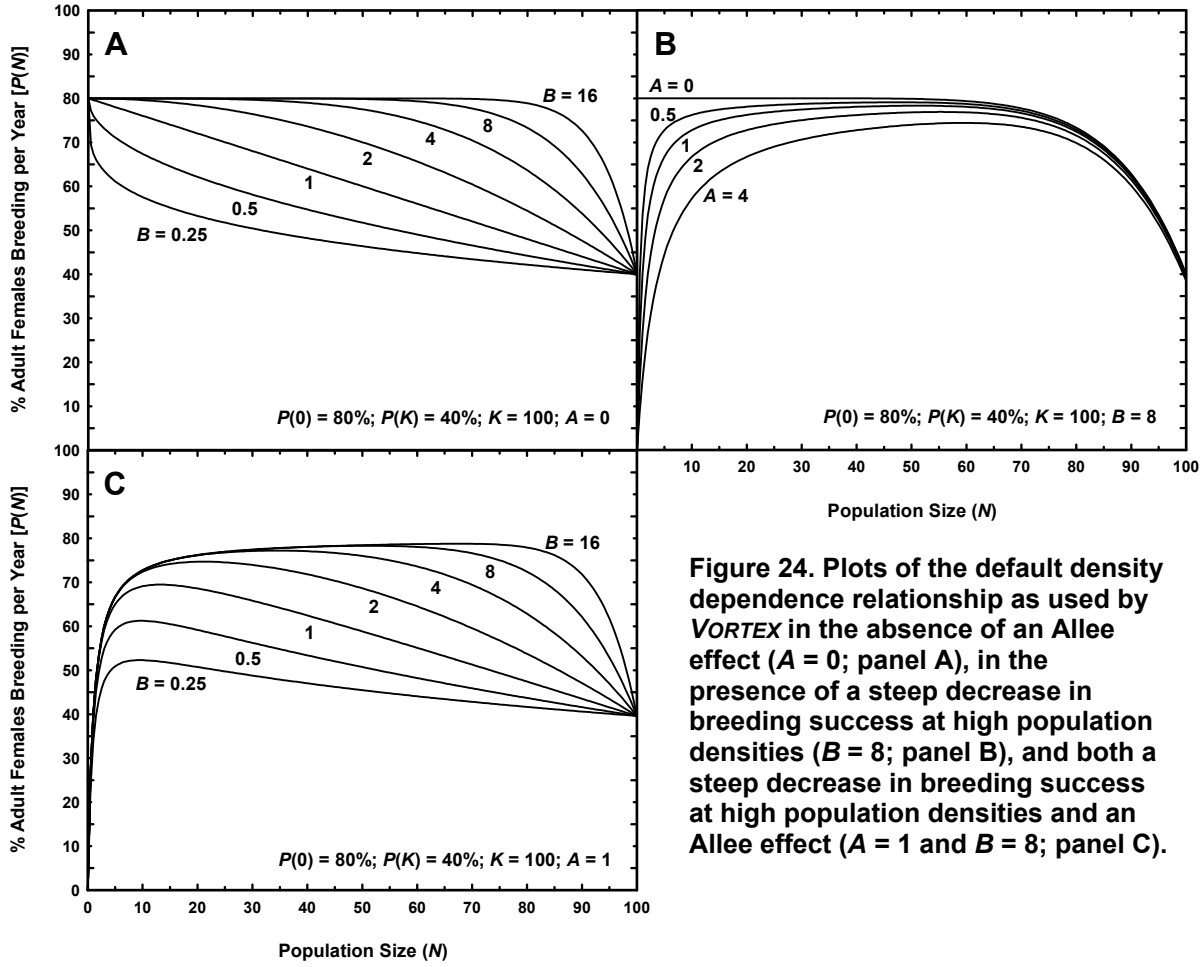


Figure 24. Plots of the default density dependence relationship as used by *VORTEX* in the absence of an Allee effect ($A = 0$; panel A), in the presence of a steep decrease in breeding success at high population densities ($B = 8$; panel B), and both a steep decrease in breeding success at high population densities and an Allee effect ($A = 1$ and $B = 8$; panel C).

formulation. Fowler (1981) suggests that density dependence in reproductive success can often be modeled quite well with a quadratic function, that is, with $B = 2$.

It is best to derive the values of $P(0)$, $P(K)$, A, and B from a regression analysis of data on the breeding rate of your population. If these data are unavailable, but you can estimate $P(0)$ and $P(K)$, then you may want to explore several different combinations of A and B to come up with a curve that seems appropriate for your population. You could use graphics or statistical software—or even graph paper and a calculator—to construct a range of hypothetical curves, using different combinations of parameters, as was done to produce Figure 24. In any event, once you have decided on a particular set of parameters to use you should always graph the resulting curve to verify that it represents the mode of density-dependent behavior you are looking for. After you have entered the appropriate parameters as shown on Figure 25 below, *VORTEX* can display a graph of the specified density dependence function for you so that you can verify the intended nature of the relationship. Select the population from the drop-down list and then hit the "View" command to see your graph. (Note: you will need to specify at the bottom of the graphing box that you want to plot the function against the 'N' parameter.)

Depending on the shape of the density dependence curve you have specified, and the mortality rates you will enter later, your population may never be able to reach the carrying capacity *K* (also to be specified later). The combination of density-dependence in both reproduction and survival will determine over what range of sizes the population is expected to experience average net growth and over what range it would be expected to decline since deaths outnumber births.

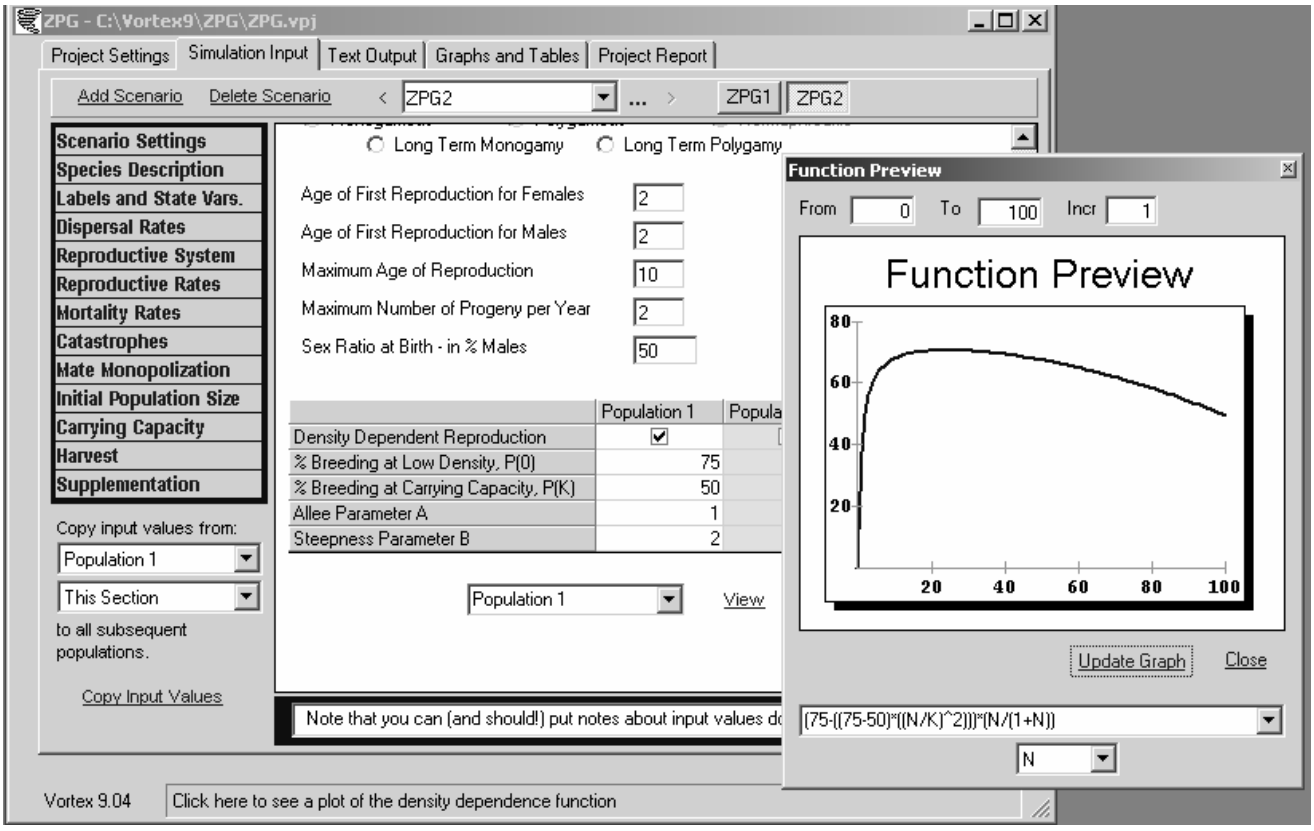


Figure 25. Specifying and graphing density dependence.

Case Study VII:
Modeling density dependence in reproductive success

Peary caribou (*Rangifer tarandus*) are distributed in fragmented populations across the Canadian Arctic. These animals are continually stressed by food resource limitation in the harsh winter climate, with this stress becoming magnified as population density increases. Consequently, a risk analysis conducted on this taxon (Gunn et al. 1998) included density-dependent reproductive success at high population densities (Allee effects were not considered to be a factor). Field data show 80% of adult females are able to breed under optimal density conditions, while only 10% are expected to be successful when the population reaches carrying capacity. In other words, $P(0)$ = 80% and $P(K)$ = 10%. To approximate the expected shape of the density dependence curve modeled in *VORTEX*, the exponential steepness parameter B was set to 4. The functional form of this relationship is shown in the top panel of Figure V-1.

In contrast, the winged mapleleaf mussel (*Quadrula fragosa*) inhabits isolated stretches of the St. Croix River in Minnesota and Wisconsin (United States), with individuals separated from one another by as much as 20-25 meters. While no evidence points to a suppression of reproductive success at higher densities, the mode of reproduction in these mussels suggests that Allee effects may play a major role in influencing reproduction as population size (and density) declines (Kjos et al. 1998). In fact, reproductive success is thought to drop off rapidly as populations are reduced to below about 30% of the estimated carrying capacity. To model this phenomenon , $P(0)$ =, $P(K)$ = 19.4%, and A = 4 (the exponential steepness B is set to zero when reproductive success is unaffected at high densities). This relationship is shown in the bottom panel of Figure VI-1.

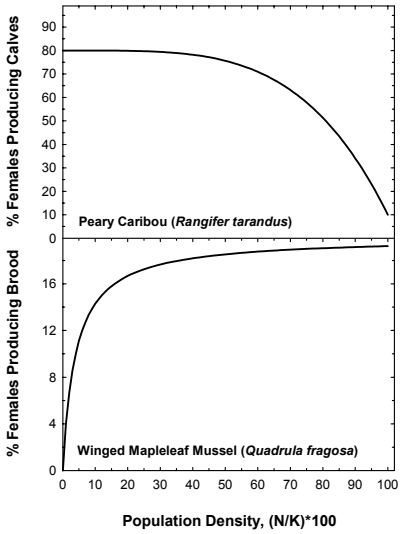


Figure 26. Density dependence functions as modeled in *VORTEX* for Peary caribou (top panel: Gunn et al. 1998) and the winged mapleleaf mussel (bottom panel: Kjos et al. 1998).

Reproductive Rates

The next section of input (Figure 27) asks for parameter values that specify reproductive rates. Note that you decide when in the development of the next generation the "birth" is defined to occur. For mammals, you would probably use parturition as the point at which offspring are tallied. For oviparous species, however, you can start to tally offspring at egg-laying, or at hatching, or at fledging, or at any other developmental stage that makes sense to you and for which you can specify the demographic rate parameters. For amphibians, you may choose to start each animal's life in the *VORTEX* model at metamorphosis. Whenever you define an individual's life to begin, you must make sure that the first year mortality rates you specify in the next input section are appropriate for the choice you made about when to start recording offspring. For example, if you tally offspring starting at hatching, then the clutch sizes you specify on this screen will be in terms of the number of hatches, and your first year mortality will be from hatching through the subsequent 12 months. If you choose to start offspring at fledging, then the clutch size will be specified in terms of the number of fledglings, and survival will be from fledging onwards.

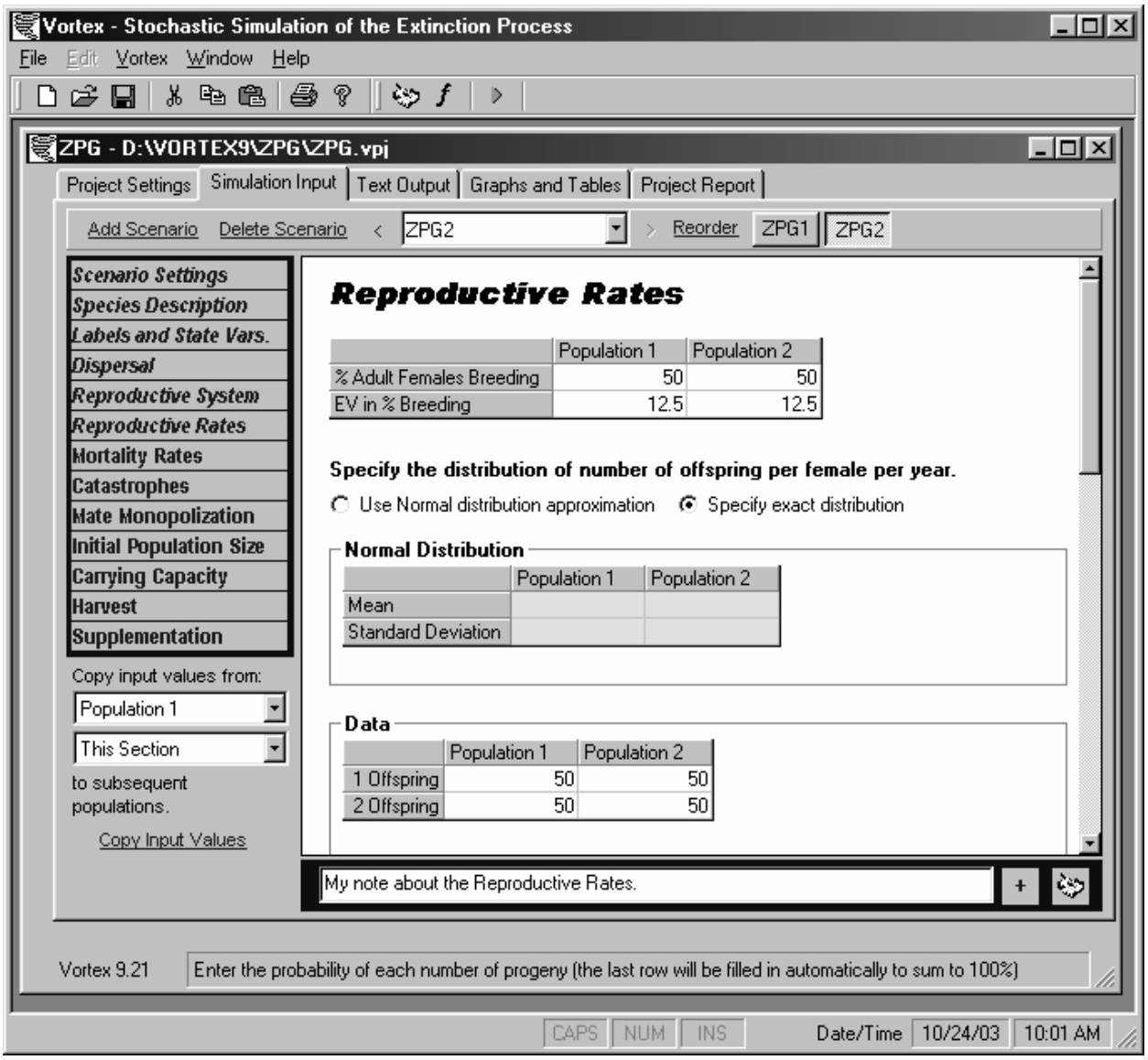


Figure 27. Reproductive Rates input section.

% Adult Females Breeding: Here you specify the mean percentage of adult females that breed in a given year (or, stated another way, the probability that a given adult female will successfully produce offspring in a given year). Data on the interbirth interval, or the timespan between successive birth events for a given female, can be useful for estimating the percentage of adult females breeding annually. A simple example: if the average length of time between successive births for adult females is 2 years, then 50% of all adult females are expected to breed in a given year (this assumes, of course, that animals can breed throughout their normal lifespan). A more detailed example is presented below in Case Study VIII.

EV in % Breeding: Environmental variation (EV) in reproduction is modeled by the user entering a standard deviation (SD) for the percent females producing litters of offspring (see Box C for a refresher on some basic concepts in statistics and their calculation). *VORTEX* then determines the percent breeding for a given year by sampling from a binomial distribution with the specified mean and standard deviation.

Case Study VIII:
Using interbirth intervals to estimate annual % adult females breeding

In a risk assessment for the Ugandan population of the eastern subspecies of chimpanzee *Pan troglodytes schweinfurthii*, Edroma et al. (1997) used interbirth interval (IBI) data from a number of well-studied populations in Uganda and neighboring countries. The mean IBI for these populations was set at 5 years. However, the early death of an infant will cause the IBI for a given female to shorten dramatically. Data suggest that if an infant dies at 6 months of age, the IBI will be reduced to about 2 years. This rapid response means that the effect of infant mortality on population growth may be quite small, so long as the mother is not killed or harmed by the same forces responsible for the death of her infant. In addition, infant mortality was set at 16%, and the frequency of non-sterile females in the population was estimated at 91%. Given these data, a corrected interbirth interval can be calculated as:

$$IBI_{corr} = \frac{(0.84)(5) + (0.16)(2)}{0.91} = 4.97$$

Based on this estimate of the interbirth interval, the percentage of adult females producing an offspring in a given year is $(4.97)^{-1}$ = 20.1%.

Box E: A Quick and Easy Way to Estimate a Standard Deviation from Scant Data

Ideally, to estimate the standard deviation of a demographic rate across years, we would want to have many years (perhaps 10 or more) of field data. However, we often have information on just a few years, and often only the best and worst years in recent times. Fortunately, the expected range observed in a sample of *n* values from a normal distribution can be specified (see below, and Rohlf and Sokal 1981). To estimate the standard deviation of a distribution, the observed range (best – worst years) can be divided by the expected range. For example, across 15 years of observations on Sonoran pronghorn antelope (Hosack 1998), the mortality rate of fawns was 85% in the worst year and 55% in the best year. Dividing the observed range (30%) by the expected range for a normal distribution (3.47 SD units), provides us with an estimate of the SD of 30% / 3.47 = 8.64%.

Table E-1. Mean ranges (in SD units) for samples of a normal distribution (from Table 26 in Rohlf and Sokal 1981)

Number of observations	Range
2	1.13
3	1.69
4	2.06
5	2.33
6	2.53
7	2.70
8	2.85
9	2.97
10	3.08
15	3.47
20	3.74
25	3.93
30	4.09
40	4.32
50	4.50

Although environmental variation in birth and death rates can have a substantial impact on the viability of a population, it is often difficult to obtain the data needed to estimate EV. Long-term field studies are needed in order to determine the amount of fluctuation that occurs in the demographic rates of your

population. If these data are available, the standard deviation in mean birth rate can be simply calculated using the methods in Box C. If your dataset is small but you are comfortable with making a rough quantitative estimate of the variability, you can use the technique presented in Box E.

A common problem in estimating annual fluctuations in demographic rates is that the data might be so sparse that it is difficult or impossible to estimate the parameters on an annual basis. If this is the case, you might be forced to admit that the data are not sufficient to allow estimation of the variability around the mean values. The only alternatives are to guess at the fluctuations in reproductive and mortality rates, based on a general understanding of the natural history of the species, or to omit environmental variability from the model altogether (by entering **0** when each standard deviation is requested). In this case, you must recognize that a potentially important component of population variability and instability is being ignored in your analysis.

Another difficulty with these approaches, which may add a significant bias if sample sizes are small, is that some of the year-to-year variation observed in reproductive and mortality rates is actually due to the expected demographic stochasticity resulting from random sampling of individuals, even if environmental factors do not cause fluctuations in the annual probabilities of birth and death. Refer to Box D for methods of removing this source of variation as a means of estimating EV alone.

In order of ease of use (easiest to most difficult) and precision (least precise to most precise), your options for estimating environmental variation (EV) in population demographic rates are: guess at the "typical" fluctuations in your species' reproduction and mortality rates; calculate the variation across years in these rates from long-term field data; adjust the observed variation by subtracting the variance due to demographic stochasticity (random sampling), even if the *probabilities* of birth and death remain constant through time.

Use Normal distribution approximation/Specify exact distribution: Previously, you defined the maximum number of offspring produced annually per female; you are must now specify the percentage of litters/clutches/broods produced by the breeding adult females that are of a given size. You have two options for specifying the distribution of numbers of progeny. You can use a Normal distribution approximation or you can fully specify the probabilities of each number of progeny. When you use the Normal approximation, *VORTEX* will randomly select a number of progeny for each breeding female by sampling from a normal distribution with the specified mean and standard deviation, and then choosing the closest whole number of offspring to the value sampled. The distribution will be symmetrically truncated, if necessary, in order to prevent the specification of negative litter sizes and to prevent bias in the sampling of the distribution.

If you have data on the percents of females producing each possible number of progeny, and if the maximum number produced is not very large, then it is more accurate to enter that exact distribution. You accomplish this by entering the percentage (i.e., a number between 0.0 and 100.0) for each specified size up to the maximum. For example, if the maximum litter size is 5 but the average litter is comprised of just 2 individuals, you would enter a much higher percentage of females producing smaller litters (say, 60% produce a litter of 2 but only 5% produce a litter of 5). The total must add to 100%, and the final value will be entered automatically by the program in order to sum to 100%.

Copy input values from: When modeling a metapopulation, you often will want to use the same values for most input parameters across all of the populations. On the left side of the Simulation Input screens is a tool that allows you to copy input values from any one population to all subsequent populations. You can copy only those values in the current Section of input, or copy values in all the input Sections.

Mortality

In this next section of input (Figure 28), you enter the age-sex specific mortalites. In the language of matrix life-table analysis (e.g., Caughley 1977; Caswell 2001), *VORTEX* defines mortality as the mortality rate q_x, or the percentage of animals alive at age x that die before reaching age $x + 1$. Enter mortality rates as a percent (between 0 and 100) for each age-sex class. Once reproductive age is reached, the annual probability of mortality remains constant over the life of the individual and is entered only once (but see Chapter 5 for further information on how to relax this assumption).

Mortality of Females (Males) as %: In these tables, enter the mean mortality rates for each age class, and enter also a standard deviation (SD) for each mean to describe the environmental variation (EV) in each rate. For information on the calculation and statistical treatment of variance in demographic parameters used in *VORTEX*, see Boxes C and D.

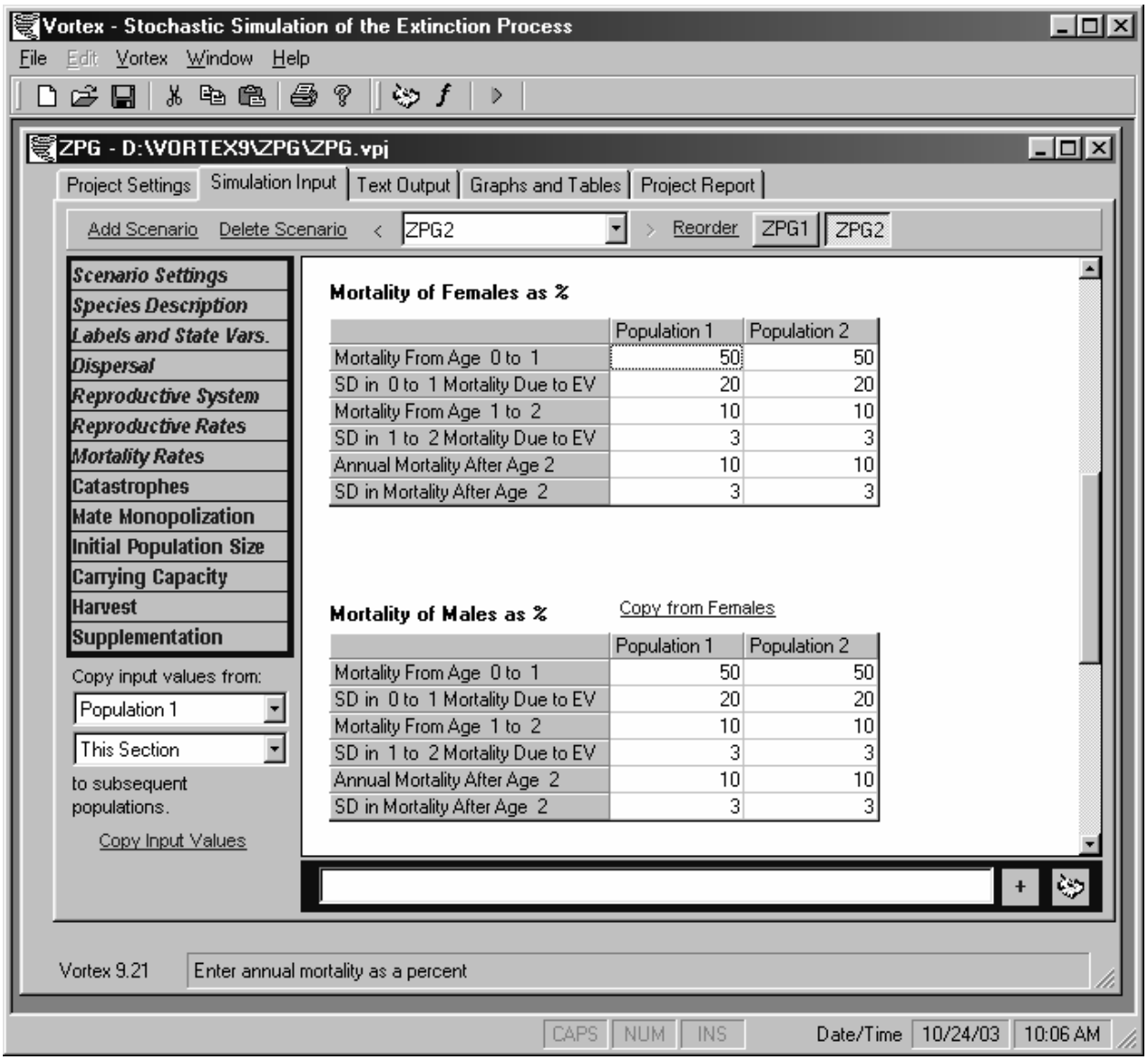


Figure 28 Mortality Rates input section.

Be aware that if you enter a standard deviation for each mean mortality rate that is at least half of the *survival* rate (100% - mortality rate) – in other words, the coefficient of variation in survival is at least 50% – in occasional years the mortality rate will be set at 100% and the population will immediately go extinct. For example, if all age-specific mortality rates are 50% and the standard deviations are set at 25%, then in about 1 in 40 years the mortality rate after adjustment for EV will be 100% (since the rate will exceed the mean by 2 standard deviations about 2.5% of the time).

A substantial literature exists on the many methods by which one can estimate age-sex specific mortality rates in wild populations; Caughley (1977) is a good text from which to start an exploration of this body of information.

Case Study IX:

Estimating mortality rates from sightings of banded Whooping Cranes

As of 1991, the last remaining population of the whooping crane (*Grus americana*) could be tracked and censused from its breeding grounds in Wood Buffalo National Park (Alberta, Canada) to its wintering grounds along the Texas Gulf Coast at Aransas National Wildlife Refuge. During a Conservation Viability Assessment for this population, Mirande et al. (1991) estimated mortality rates for the population based on recorded sightings of banded birds. From 1976 through 1989, about 234.5 cranes were observed to hatch at Wood Buffalo NP (taking the midpoint of the possible range in those few years in which counts were imprecise), of which 172 arrived in Aransas the following winter. This yields an estimated juvenile survival rate of 73.3%. During the 14 years of close monitoring of the Wood Buffalo population, the observed variance around the mean survivorship of 0.733 was 0.047. The variance that would be expected from random binomial sampling based on this mean is 0.013. The difference (V = 0.034, or SD = 0.184) can be attributed to environmental variation.

Mortality after the first year can similarly be determined from either data on banded birds of known age, or from winter census reports from Aransas filed since 1938 (young of the year are distinguishable from older birds upon arrival at Aransas). Since 1938, a total of 2359 birds older than 1 year of age returned to Aransas, out of a total of 2594 birds that departed Aransas the previous spring. This yields an estimated annual mortality after the first year of 9.06%. Among the banded birds, 89.9% annual survival was observed in 386 bird-years, but band loss after several years could have accounted for some of the "mortality" recorded among banded individuals. No variation was detectable statistically among mortality rates calculated separately for each age class beyond the first year.

The observed annual variation in survival rates from 1938 to 1990 was V = 0.00255; the variation expected due to binomial sampling from a constant probability is V = 0.00220. The difference can be attributed to environmental variation in the probability of surviving, with V = 0.00035, or SD = 0.019. This value turned out to be very close to the intuitive estimate provided by workshop participants – that annual fluctuations in mortality rates would be about ± 2%.

Catastrophes

In the next section of input (Figure 29), you enter data to characterize catastrophes that might strike your populations. Note that you must do this for each type of catastrophe you identified (back in the Species Description section) across each population comprising your metapopulation (if you are modeling more than one population). You toggle among the types of catastrophes by clicking on the buttons arrayed across the top of the Catastrophes window.

Don't forget to enter data for Catastrophe 2 (if any) and all further catastrophes after you have completed entering data for Catastrophe 1.

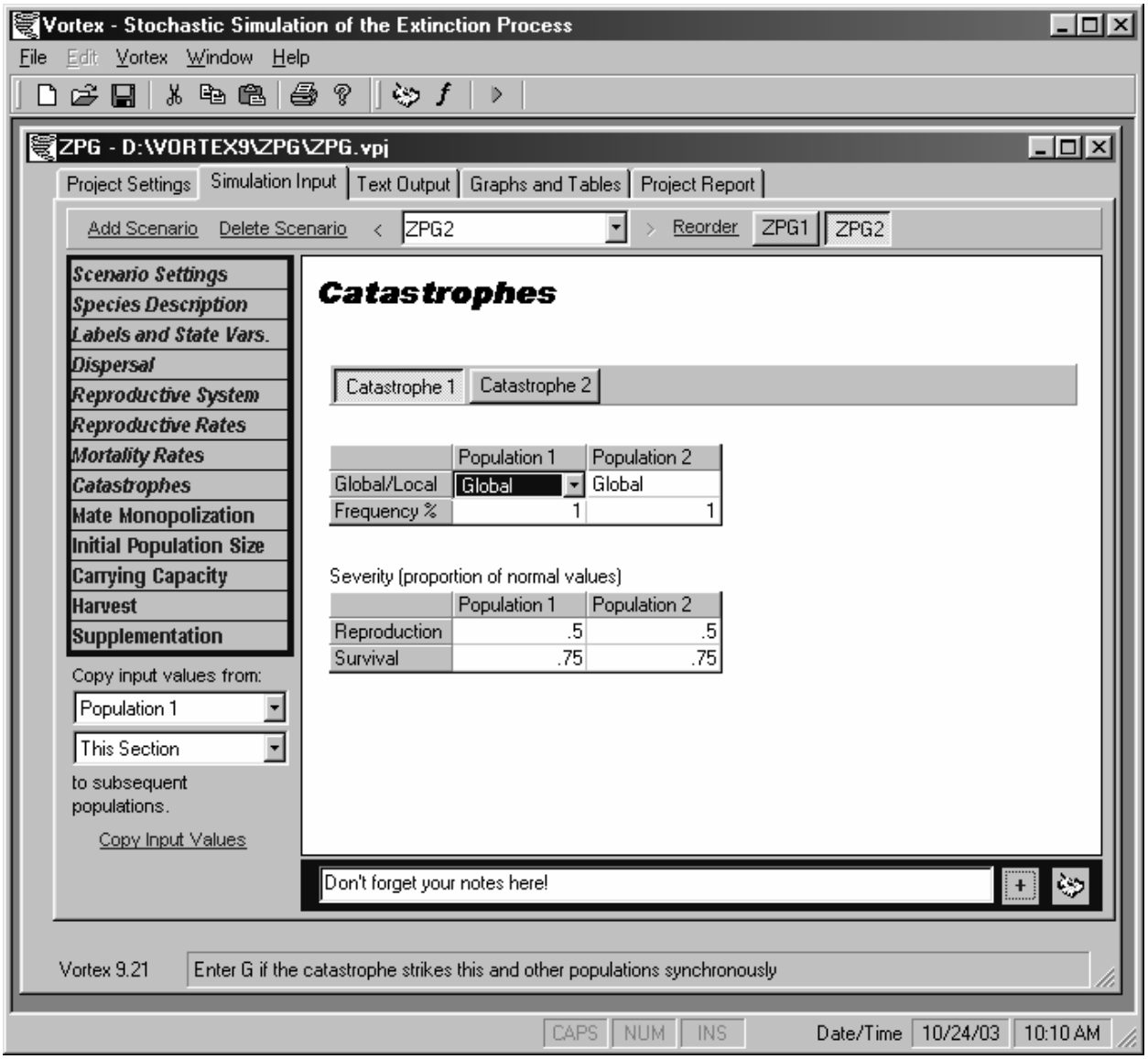


Figure 29. Catastrophes input section.

Global/Local: Each catastrophe is to be specified as global or local in scope (this is applicable only when more than one population is modeled). You are given considerable flexibility in how the scope of each catastrophe is specified, so it is important to read the following information carefully in order to correctly model your metapopulation.

A *global* catastrophe will occur in the same years in all populations, but the severity of effects can be entered as different or equal across populations. *Local* catastrophes occur independently among the populations.

To cause a catastrophe to be *regional* in scope, affecting only a subset of the populations, you can specify that it is global, but then set the severity factors to 1.0 (see below) for those populations which are not affected by that regional catastrophe.

You may also specify that a catastrophe is global for some populations, but local for others. In that case, the catastrophe happens concurrently across the populations for which it is global, but occurs independently in those populations for which it is local.

Normally, the frequency of a global catastrophe would be set to be the same in each population affected by that global catastrophe. However, you can specify different frequencies for a global catastrophe among the populations. In that case, when the catastrophe hits a population, it will also hit all other populations in which that catastrophe has at least as high a frequency of occurrence. The catastrophe will sometimes occur in the populations that have higher frequencies while not occurring in populations with lower frequencies.

Case Study X:
A "catastrophe sampler"

1. Attwater's Prairie Chicken

The impact of hurricanes was assessed by Seal (1994) in a Population and Habitat Viability Assessment for Attwater's prairie chicken (*Tympanuchus cupido attwateri*), an endangered bird that was reduced to just 3 disjunct subpopulations in coastal southeastern Texas. Based on data from the National Oceanic and Atmospheric Administration, it was assumed that hurricanes strike this area on average once every 70 years. Species biologists indicated that populations in Refugio County dropped from 1,200 – 1,500 in the spring prior to Hurricane Beulah to approximately 250 in October following that storm. Therefore, it was assumed that catastrophic hurricanes would result in 80% mortality of the adult (post-fledging) population. This would translate into a severity factor with respect to survival of **0.20**. Because hurricanes typically occur during late summer and autumn, it was assumed that such an event would not affect reproductive success as breeding occurs in the spring.

2. Winged Mapleleaf Mussel

Kjos et al. (1998) identified major upriver chemical spills as the primary catastrophe impacting the last surviving populations of the winged mapleleaf mussel, *Quadrula fragosa*. A chemical spill of this type could occur as a result of, for example, an accident involving a vehicle carrying hazardous materials. A detailed analysis by the Minnesota Department of Transportation suggests that the probability of such an event could be quite small (see Kjos et al. (1998) for a detailed description of the calculation). A very conservative estimate of the probability was set at 0.20%; i.e., it is thought to occur perhaps, on average, once every 500 years. However, if it were to occur, it would have major effects on the mussel populations: in the year that such an event occurs, both reproductive success (proportion of adult females breeding) and survival (spread out across all age classes) would be reduced by 30%, equivalent to a pair of severity factors equal to **0.70**.

3. Mountain Gorilla

The primary catastrophic event modeled by Werikhe et al. (1998) in their evaluation of mountain gorilla (*Gorilla gorilla beringei*) viability was the spread of disease from humans to gorillas. As the extent of human-gorilla interaction increases with rising human population pressures, the likelihood of passing human diseases to gorillas is thought to be markedly higher. Data from discussions with primate veterinarians at the PHVA Workshop led to the construction of the following major disease events:

- Influenza-like disease – 10% annual probability of occurrence; 5% reduction in survivorship; no effect on reproduction
- Severe, but not pandemic, viral disease – 10% annual probability of occurrence; 25% reduction in survivorship; 20% reduction in the proportion of adult females breeding
- Hypothetical viral disease with chronic cyclicity, targeting the organ reproductive system – 4% annual probability of occurrence; 25% reduction in survivorship; 100% reduction in the proportion of adult females breeding (i.e., no reproduction during a catastrophe year).

Frequency %: Once the scope of the catastrophe is identified, you need to define the probability that a given catastrophe will occur in a particular year. Enter this as a percent from 0.0 to 100.0. For example, a value of **1.0** means that there is a 1% chance that this particular event will occur in any one year. Stated another way, a catastrophe given a frequency of occurrence of 1.0% means that, in a simulation lasting 100 years, this event is expected to occur one time on average.

Severity (proportion of normal values): For each catastrophe, you need to define the severity with respect to reproduction (percentage of adult females breeding) and survival. The fecundity and survival rates for years in which a catastrophe occurs are obtained by multiplying those rates in a "normal", non-catastrophe year by the specified factor. These severity factors range from 0.0 to 1.0. Entering **0.0** indicates a total loss of reproduction or survival for the population and **1.0** means that the catastrophe, when it occurs, will have no effect. For example, entering **0.75** for the severity factor with respect to reproduction means that, if 50% of adult females breed in a normal year, then only (50%)(0.75) = 37.5% breed in a year with a catastrophe.

Catastrophe severity factors greater than 1.0 can be used in your model. This would result in "catastrophes" having beneficial effects on reproduction and/or survival.

Mate Monopolization

You are now asked to specify the male breeding characteristics of your population. This information is important for those species that may have an established social structure and, consequently, exclude some adult males from the pool of available breeders. The look of this screen (Figure 30) will depend on whether you specified Monogamous or Polygamous breeding back in the Reproductive System section.

If you previously specified that the breeding system in your population was polygynous, you must specify how many of the males are breeders. To describe the degree of polygyny, you will need to provide an value in one of the following three lines of the grid:

a) % Males in Breeding Pool
b) % Males Successfully Siring Offspring (producing at least one offspring in the average breeding cycle or year)
c) Mean # of Mates/Successful Sire (the mean number of litters sired by successful males in each year)

Whichever one of the three parameters you specify, *VORTEX* will calculate the other two values based on the assumption that some males are excluded from the breeding pool and breeding success among males in the pool of available breeders is described by a Poisson distribution. Only the top number is actually used in the simulation model; the other two are provided as alternative ways to enter the degree of polygyny.

If you earlier specified that the species has a monogamous breeding system, you are asked specify only the percentage of the total adult male population that makes up the pool of available breeders (and each male can breed with only one female each year). Remember that not all males within this pool may breed in a given year, depending on the number of adult females that are successful breeders.

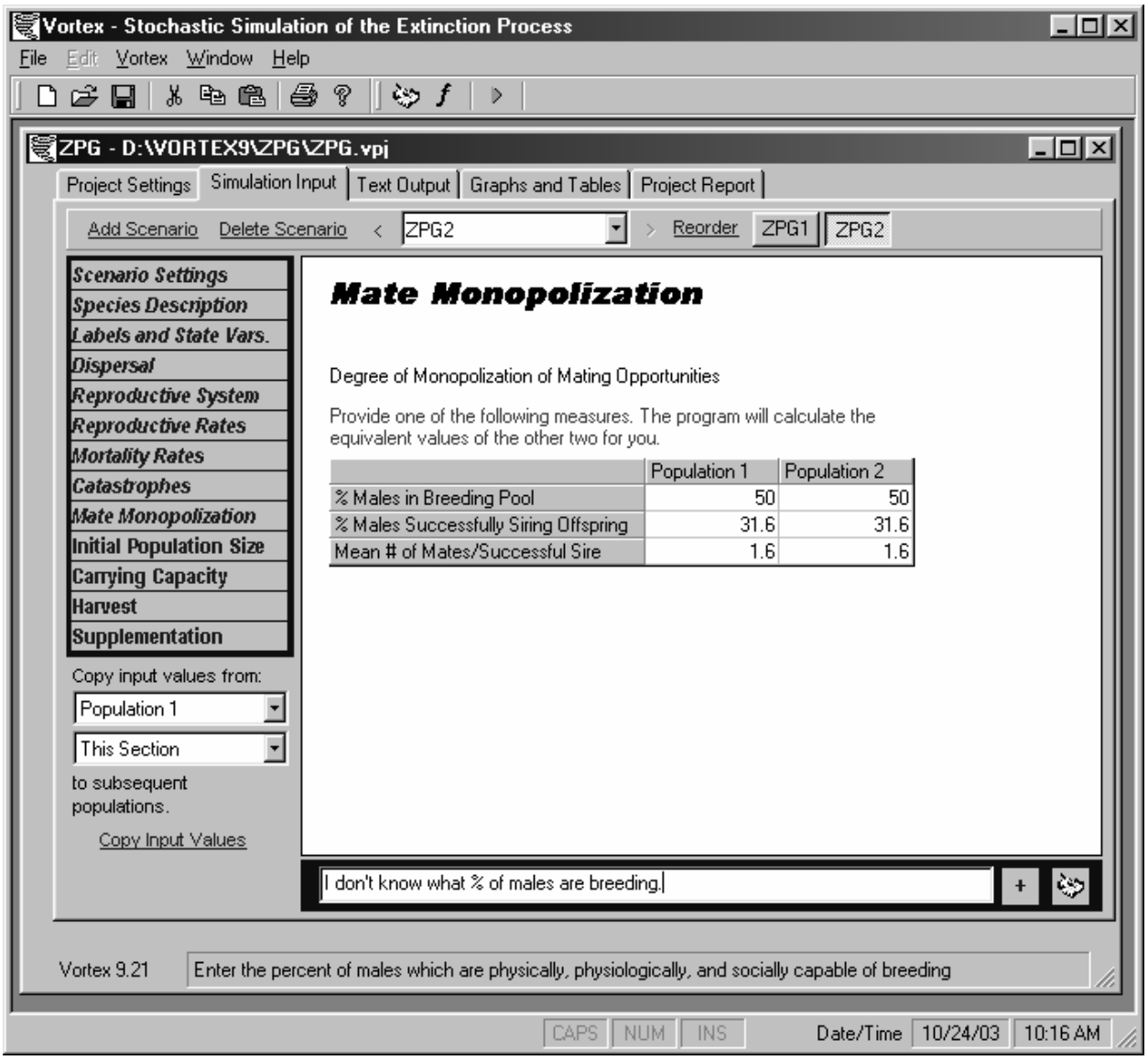


Figure 30. Mate Monopolization input section.

Initial Population Size

In this section of input (Figure 31), you specify the number of individuals at the start of your simulation.

Stable Age Distribution/Specified Age Distribution: You have two options for entering initial population sizes. If you do not know the precise age-class distribution in your population (as is usually the case), you can initialize your population according to the *stable age distribution* (see Box G in Chapter 4 for a definition of and methods for calculating this distribution). If you select the stable age distribution, you then enter the total *Initial Population Size* for each population. *VORTEX* will assign individuals to each age-sex class proportionate to the stable age distribution, and will show that distribution in the grids.

If instead you choose to enter a *Specified Age Distribution*, you will then enter the actual size of each age class for both males and females. You may need to use scroll bars to view the older age classes in the grids. As you enter these values, you will notice that the total initial population size changes accordingly.

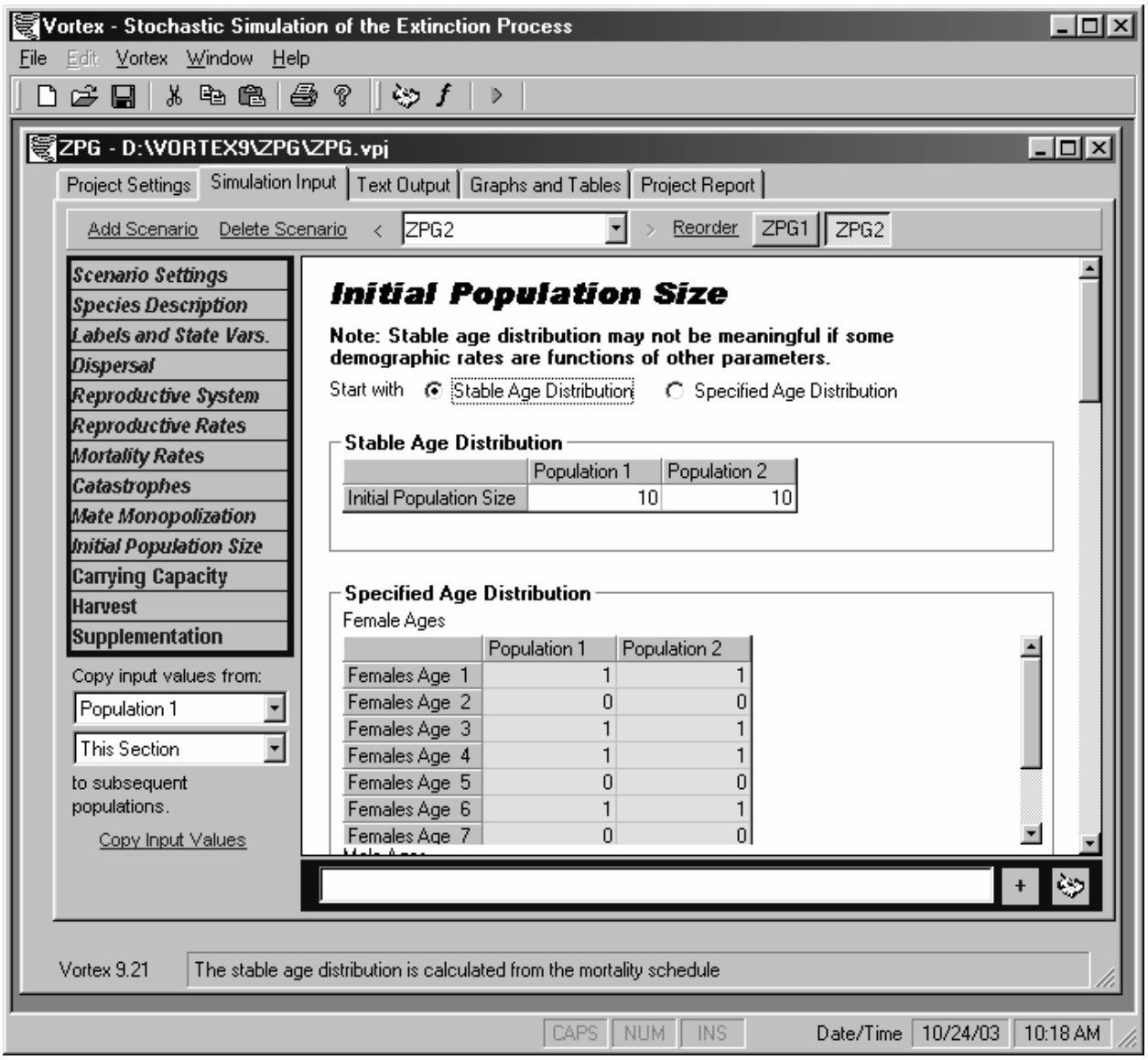


Figure 31. Initial Population Size input section.

Carrying Capacity

(see Figure 32)

Carrying Capacity (K): The carrying capacity describes the upper limit for the size of your simulated population within a given habitat and must be specified by the user in this next section of input (see Box F for a more in-depth discussion of this parameter). If the population size *N* exceeds *K* at the end of a particular time cycle, additional mortality is imposed across all age and sex classes in order to reduce the population back to this upper limit. The probability of any animal dying during this truncation process is set to ($N - K / N$), so that the expected population size after the additional mortality is *K*.

SD in K Due to EV: If you think that the habitat carrying capacity varies over time due to environmental variation (EV), you can enter a standard deviation (SD) here to account for this variability. For example, the habitat might support different population sizes in different years due to changing conditions such as rainfall or food resources. The standard deviation should be entered as a number of animals, not as a percentage of *K*; for example, if $K = 2000$ with a standard deviation of 10%, then enter **200**.

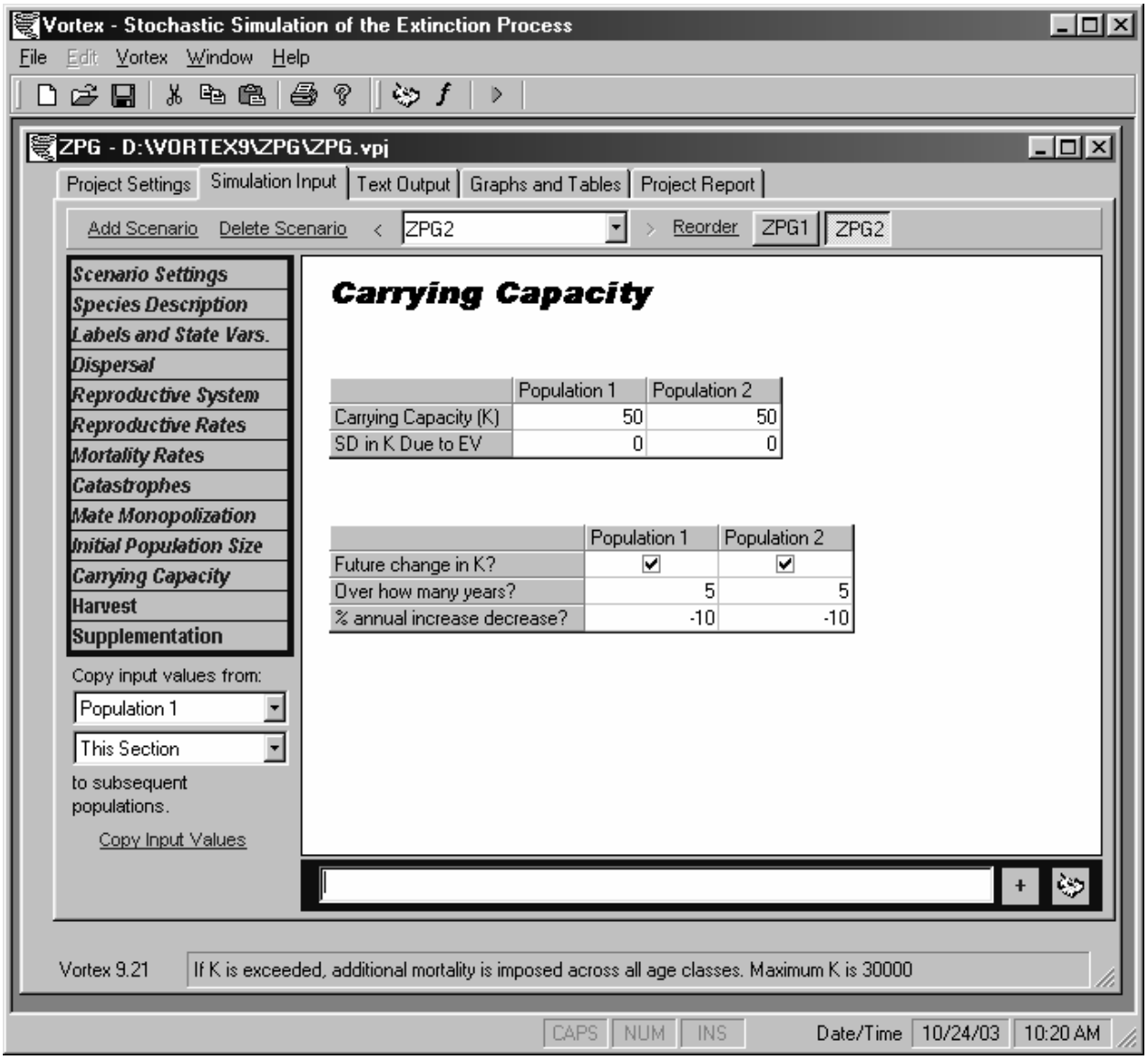


Figure 32. Carrying Capacity input section.

Be careful! If you enter a standard deviation for the carrying capacity that is greater than *K*/3, then the value for *K* could drop to zero during your simulation – resulting in an unwanted extinction event. If you're not convinced, see Box C for an explanation of why this is so.

Trend in K? *VORTEX* allows you to simulate changes in the carrying capacity. Such changes may be positive or negative and result from human activities such as resource utilization or corrective management strategies, or from intrinsic ecological processes such as forest succession. To include a trend in carrying capacity, check the box. Then specify the time period during which the trend will occur, and the annual rate of change in *K*. The trend will begin in year 1 and continue for the specified duration. The program will model a liner trend over this time period. Note: more complex patterns of changing K can be specified by entering a function in the box for Carrying Capacity (see Chapter 5).

Box F: What Exactly *Is* Carrying Capacity, Anyway?

"Carrying capacity—rarely in the field of resource management has a term been so frequently used to the confusion of so many."
(MacNab 1985)

The definition and use of the concept of carrying capacity is one of the more tricky issues in population viability analysis (and, for that matter, in much of population ecology). Pick up any number of textbooks on ecology or wildlife management and you are likely to find that each one presents a slightly different formal definition of carrying capacity. In fact, some authors (e.g., Caughley 1977) choose not to use the term altogether in their presentation of the mathematics of population growth. In the context of wildlife management, the habitat carrying capacity for a particular population can be defined as the maximum number of individuals that environment can sustain over time in the absence of unnatural disturbances, and without inducing harmful trends in the abundance of the resources required by that population.

We can gain more insight into this concept by considering the familiar (and admittedly simplistic) logistic equation for population growth:

$$\frac{dN}{dt} = rN\left[\frac{K-N}{K}\right]$$

where *r* is the intrinsic rate of population increase, *N* is population size, and *K* is carrying capacity. Mathematically, *K* can be thought of as the population size limit at which the rate of growth *dN*/*dt* is equal to zero. Some ecologists define *K* as a ratio of the total rate of food production in the habitat (*P*) to the per capita rate of food consumption necessary for survival (*M*). Since a population of size *N* must consume food resources at a rate of *NM* just to stay alive, there are *P* – *NM* resources available for the production of new individuals. If *NM* exceeds *P*, then resources available for reproduction become negative and the population must decrease in size.

When N is very small—for example, when a population is re-established in its native habitat—the potential growth rate is very close to exponential. If the population exceeds its carrying capacity, the number of individuals will be reduced until $N \leq K$. The carrying capacity, then, can be thought of as representing a stable equilibrium population size. Many population ecologists describe the gradual approach towards this equilibrium in terms of *damped oscillations* in population growth.

Empirically, one could estimate the habitat carrying capacity for a given animal species by calculating the total food supply appropriate for that species that is available in the habitat, and dividing that value by the rate of that species' consumption of its available food supply (for a detailed discussion of this technique, see Hobbs and Swift (1985)). For example, Petit and Pors (1996) estimated population sizes, flower availability and nectar output for each of three species of columnar cacti on Curaçao. Carrying capacities for the two species of nectar-feeding bats dependent on these cacti could then be estimated based on the daily availability of mature flowers and the field energy requirements of the bats, with additional energy requirements associated with pregnancy and lactation taken into account.

If detailed data such as these are unavailable, a rough estimate of habitat carrying capacity can be generated using long-term data on population size. If the size of the population of interest appears to be relatively constant over the period of observation (and in the absence of significant human impact), one can fairly safely assume that the population is at or near its carrying capacity. If this equilibrium is observed in the presence of major human influences, such as a strong hunting pressure, then historical data could be consulted to determine if this stable size is indeed natural or purely artificial. One could also calculate *K* for a given habitat using population density data from undisturbed habitats elsewhere in the species' range.

Harvest

In this section, *VORTEX* gives you the option of removing individuals during a simulation (Figure 33).

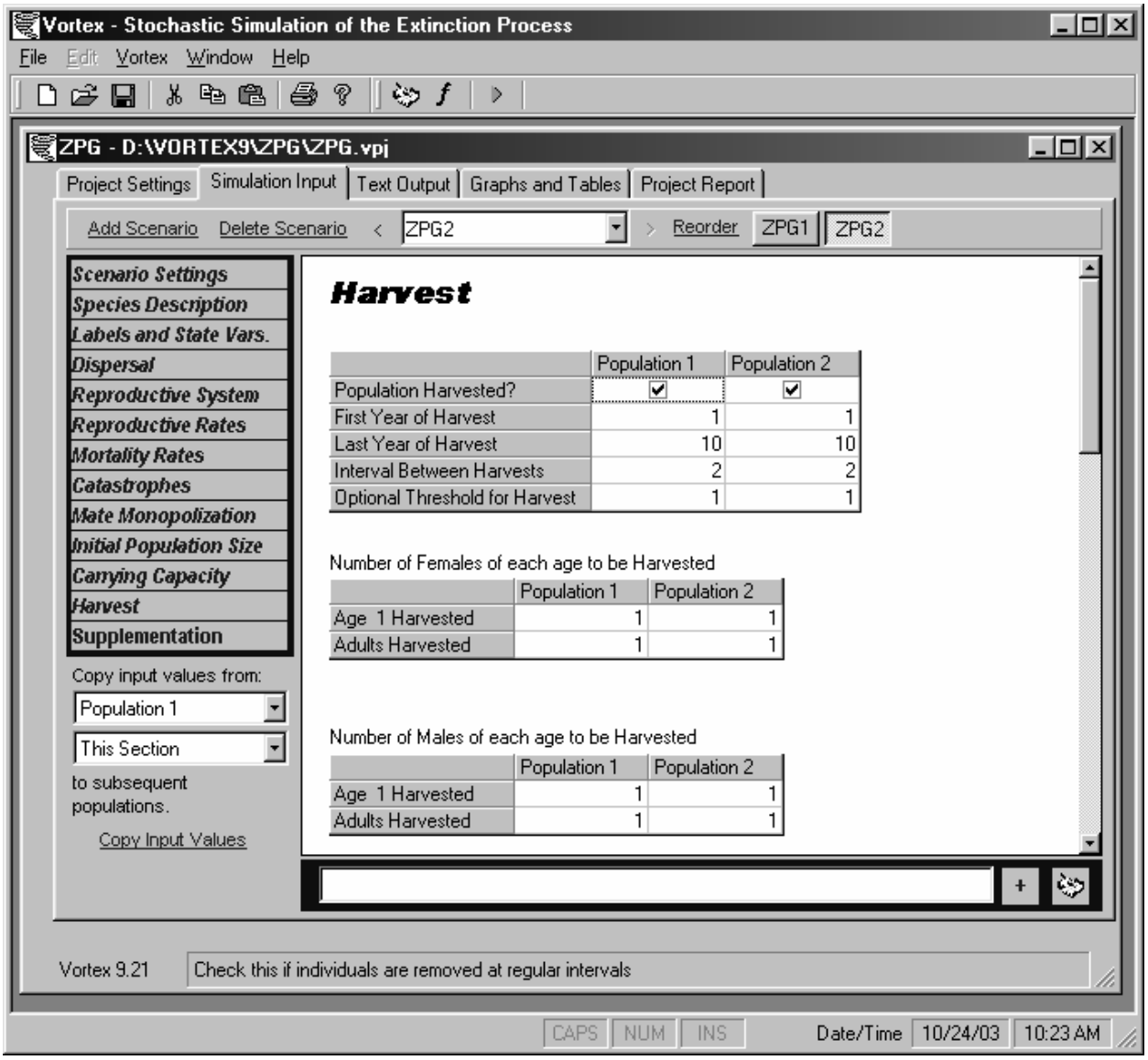


Figure 33. Harvest input section.

Harvest can mimic hunting, culling, research-related removals, removal of young individuals for translocation programs, etc. Check the *Population Harvested?* box to request a regular harvest of individuals.

The harvest can begin and end at any time during the stipulated length of the simulation. Enter the *First Year of Harvest* and the *Last Year of Harvest*. For example, if you wish to begin harvesting in year 10 and end in year 25, enter **10** and **25** for these two questions, respectively. No harvest will be allowed before or after the time frame that you have specified.

If you wish to harvest every year within the specified time frame, enter **1** for the *Interval Between Harvests*. If you wish to harvest animals every other year, enter **2**. As another example, if the first year of harvest is 10, the final year is 50 and the interval is 10 years, then harvesting will take place in years 10, 20, 30, 40 and 50.

Optional Threshold for Harvest: You can specify here some criteria that will restrict harvesting to occur only if the population status meets certain conditions. You enter this as a function (see Chapter 5). For example, if you enter "**=(N/K)>0.8**" then harvests will only occur if the ratio of the population size to the varying capacity is at least 0.8 (and if it is a harvest year as defined above). Leave the grid cell entry as **1** if you do not want to provide any harvest threshold criteria.

Female (Male) Ages being Harvested: Enter the number of females and/or males that you will harvest at each time interval defined for each age class through adults. Enter **0** for no individuals to be harvested in a given age class. *VORTEX* will conduct the harvest immediately prior to calculating the year's breeding pairs, so the youngest individual that can be harvested is one year old. If the program attempts to harvest individuals from an age class and finds an insufficient number of individuals, the simulation will continue without the harvest of those individuals determined not to exist. *VORTEX* will then report at the end of the simulation that some of the attempted harvests could not be carried out.

Supplementation

You also have the option of adding any number of juvenile or adult, male or female individuals to each population (Figure 34). This option can simulate supplementation through, for example, a translocation or releases from a captive breeding program. As with the harvest option, supplemental individuals can be added at any time and interval within the specified time frame for the simulation. Furthermore, you are allowed to both harvest and supplement individuals in a fashion independent of one another.

VORTEX assumes that the individuals that are being added to the recipient population are unrelated to both each other and to any other individual in the recipient population. Consequently, supplementation is a means of increasing genetic diversity as well as total numbers of individuals within a population.

If you want to supplement your population(s), check the *Population Supplemented?* box. You must then provide the values on the subsequent lines to define the nature of the supplementation.

First (Last) Year of Supplementation: The supplementation can begin and end at any time during the stipulated length of the simulation. Enter the years in which you wish to begin and end supplementation. For example, if you wish to begin supplementing in year 20 and end in year 50, enter **20** and **50** for these two questions, respectively. No supplementation will be allowed before or after the time frame that you have specified.

Interval Between Supplementations: If you wish to supplement every year within the specified time frame, enter **1**. If you wish to supplement every other year, enter **2**.

Optional Criterion for Supplementing: You can specify here some criteria that will restrict supplementation to occur only if the population status meets certain conditions. You enter this as a function (see Chapter 5). For example, if you enter "**=(N/K)<0.25**" then supplements will be added only if the ratio of the population size to the varying capacity is at less then 0.25 (and if it is a supplementation year as defined above). Leave the grid cell entry as **1** if you do not want to provide any criterion for supplementing.

Female (Male) Ages being Supplemented: Enter the number of females and/or males that you will add at each time interval defined for each age class through adults. Enter **0** for no individuals to be supplemented in a given age class. These parameters differ slightly from the partameters defining harvesting in that the last age class listed on the screen corresponds to the first year of adulthood instead of the aggregate adult stage. This difference results from the fact that while harvesting selects any adult individual regardless of age, *VORTEX* must assign a specific age class to each adult that is being added to

the recipient population. The age of adults added to the population is always equal to the age at which breeding commences.

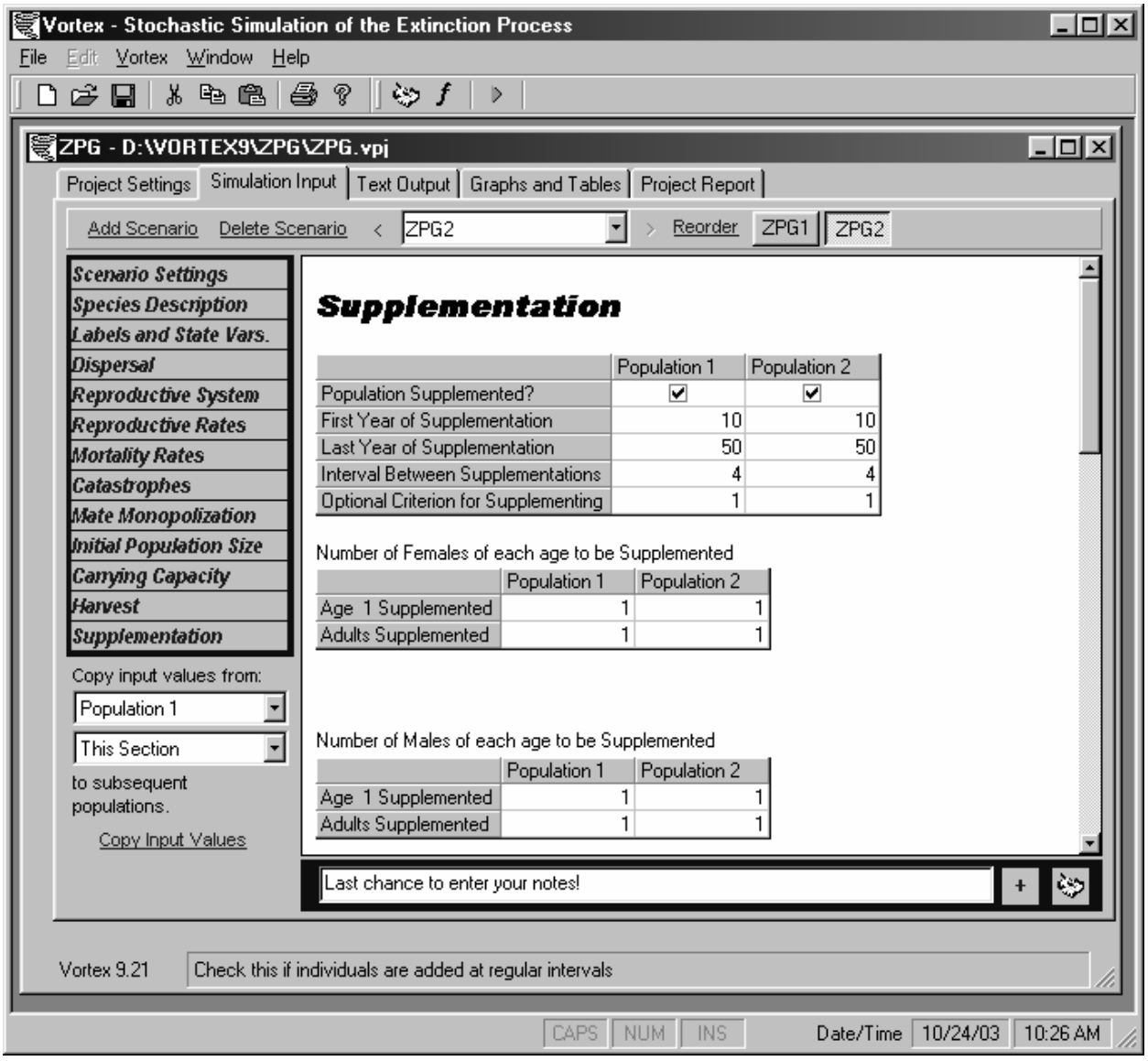


Figure 34. Supplementation input section.

Saving your Input and Running the Simulation

After you have completed entering values for all of the input parameters, it is probably wise to save your project. (You would probably be disappointed if you spent a long time entering input values, did not save them, and then the program crashed during the simulation because one number was wrong.) To save your Project, click on the save icon (the disk) on the toolbar, or select Save or SaveAs from the File menu. If you save as a file name other than what you originally specified for the Project, *VORTEX* will prompt you to find out if you wish to change the Project name to match the file name. (It makes sense to keep the file name and the project name the same, although you do not have to do so.)

To run your simulation, click on the Run icon (the green triangle) on the toolbar or select Run Simulation from the *VORTEX* menu. The Run Simulation box (Figure 35) will then appear. Check the boxes to indicate which scenario(s) you wish to run and then hit the Run! command.

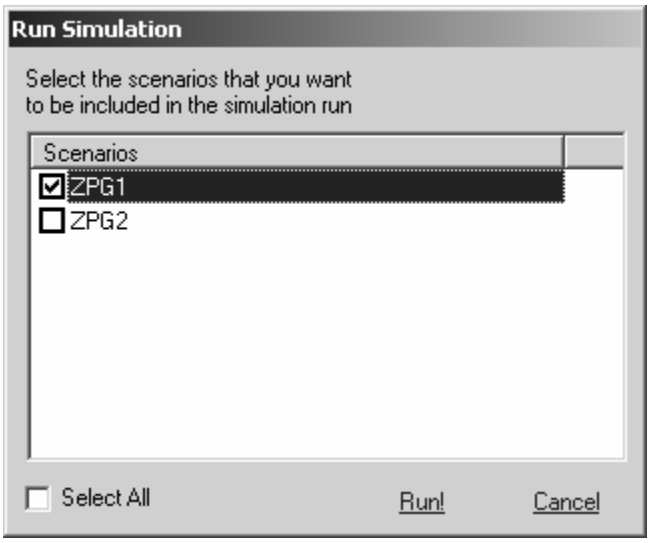


Figure 35. Run Simulation selection window.

During the simulation, a graph of the changing population size will be displayed (Figure 36). If the simulation runs slowly (as it will if you have a very large population size) you can hit buttons to *Stop*, *Pause*, or *Clear Lines*. Stopping will terminate the simulation without completing all of the iterations. Pausing will temporarily stop the simulation (as you might want to do while describing the model to others), and then will *Resume* when you hit that button (which appears after you hit *Pause*). *Clear Lines* just gives you a way to erase all prior lines if the screen is getting cluttered and unreadable.

VORTEX uses a very fast method to write all of the lines to the screen. (If they are slow, that is because the simulation itself, rather than the graphing, is taking a long time.) Consequently, the program may not refresh the display if you drag the graph window or toggle out to another Windows application and back. Therefore, it is best to not try to do anything else on your computer while the simulation is running. (This also helps by leaving all memory and system resources available to *VORTEX*.) If you feel that you must do other work (e.g., using Word or Excel or check email) while the *VORTEX* simulation is working, you should specify the Special Option (under Project Settings) of "Do not show graphs during iterations."

When the requested simulations are complete, *VORTEX* displays a few summary statistics at the top of the graph. When you are done viewing the graph, close it by clicking on the 'x' icon in the upper right corner. If you want to print or save this graph of the simulation, use the Windows PrntScrn button to copy the image to your Windows clipboard. You can then paste it into Word, or PowerPoint, or any other program that can display images. (However, data for tabulating and graphing summary results have already been saved on your disk – as we will see in the next Chapter, so there is usually no need to save these rather cluttered displays of all iterations.)

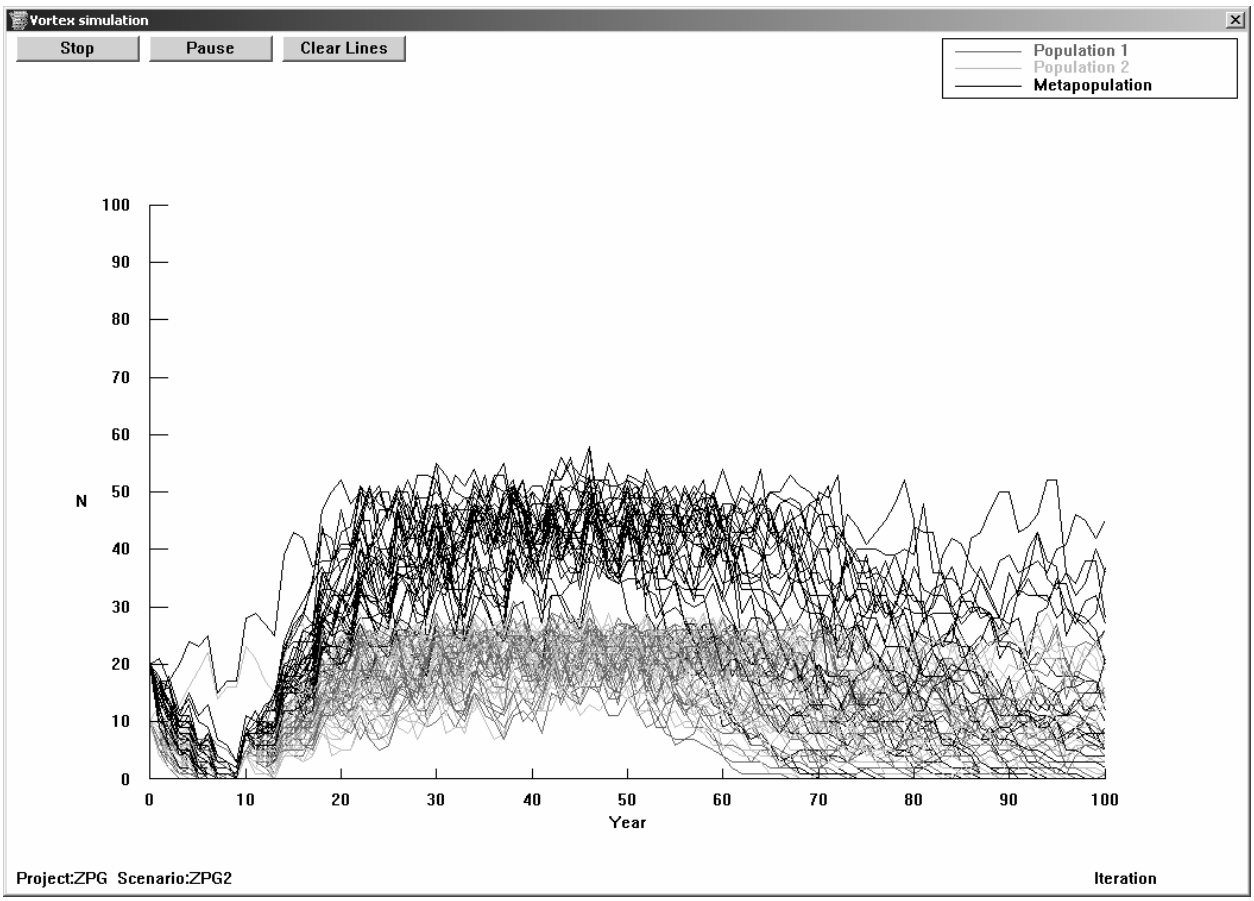


Figure 36. *VORTEX* Simulation population size graph.

Adding and Deleting Scenarios

Congratulations! You have created and run your first scenario. However, it is highly unlikely that you are now done with your analysis of the particular species, population, and issue at hand. Almost certainly, you were uncertain about some of the input parameters you entered. Possibly the estimate was based on few (or no!) data. It may be that the data came from field studies conducted in a different part of the species range. And it may be that the data are accurate descriptions of the past or even present status of the population, but are not likely to be good descriptors of the future performance of the population, in light of expected or planned changes to the habitat or populations. In any case, a major part of almost all population viability analyses is "sensitivity testing" – the examination of the impacts of varied input parameters on the projected population performance. You should refer to the background material in Appendix I and in the references for a more thorough discussion of the topic of sensitivity testing.

To conduct sensitivity testing, or any investigation of alternative scenarios that may be used to describe the population, you need to create, run, and analyze scenarios that vary from your initial case for one or a few input parameters. One way to do this would be to start from the beginning and create a new analysis in *VORTEX*. However, the program makes it very easy for you to copy all input from a prior Scenario into one or more new Scenarios in your Project. In these newly copied Scenarios, you can then change the few input parameters that you want to vary, and re-run the simulations for each case.

Adding Scenarios to Your Project

To add a scenario, from any Simulation Input window, click on the "Add Scenario" command in the upper left. The pop-up window shown in Figure 37 will appear.

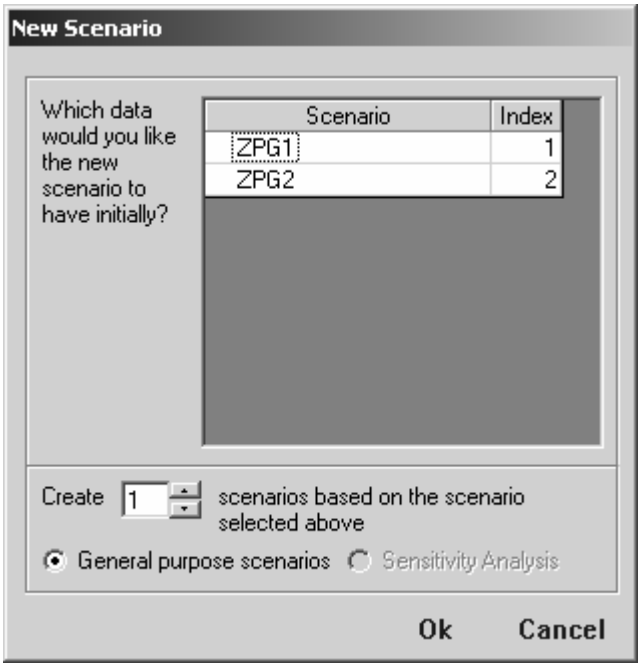


Figure 37. New Scenario window for adding Scenarios based on a prior Scenario.

Click on the existing Scenario that you want to use as a template for new Scenarios, then select below the number of copies you wish to create of this Scenario, and then click on "OK". You may notice that there

is a disabled option for "Sensitivity Analysis". This option has not yet been implemented, but it will (in a later version) provide you with a more automated way to create new Scenarios that systematically vary in one or more parameters.

The new Scenarios you create will initially be named as "Scenario1 – Copy 1", Scenario1 – Copy 2", etc., in which "Scenario1" is the name of whatever Scenario you chose to use as the template. After you create new Scenarios, you can toggle among the Scenarios in any of three ways: (1) you can use the drop-down list to select the Scenario you wish to work on, (2) you can click on the small '<' and '>' buttons alongside the dropdown list to move backwards and forwards through the list of Scenarios, and (3) you can click on the buttons to the right with the Scenario names. (See Figure 38.)

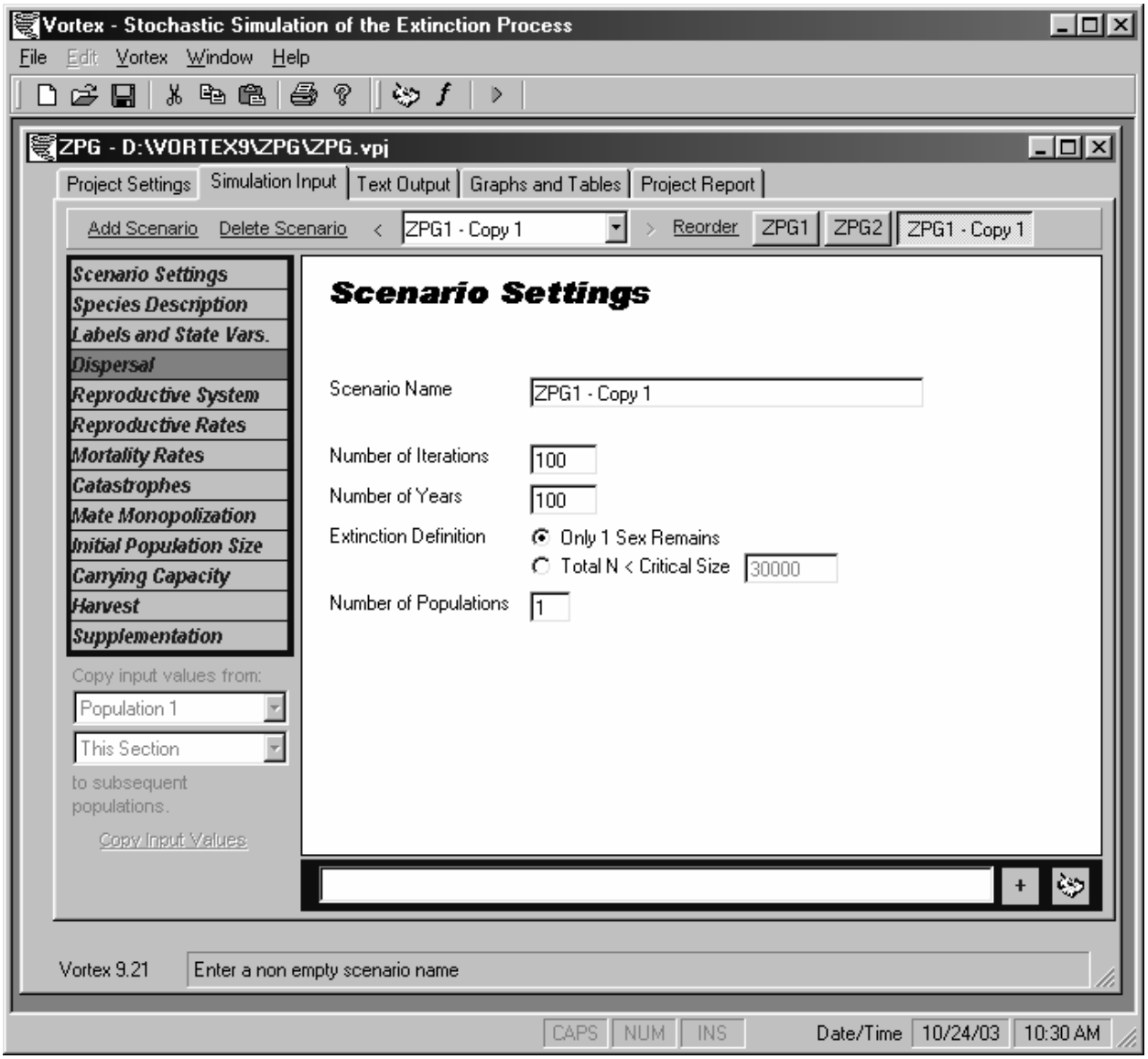


Figure 38. Multiple means for moving among alternative Scenarios.

The first task you should complete after creating new Scenarios is to change their names to something more descriptive. You do this in the top input box (Scenario Name) of the Scenario Settings screen. After

changing the Scenario name to something more descriptive, go to the Input sections where you want to vary the parameters in the new Scenarios, and make the desired changes.

Once you have many Scenarios in your Project, it is easy to accidentally change the labels and input values for the wrong Scenario, because the screens for the various Scenarios look so similar. Before you start editing input values, make sure that you are working on the intended Scenario.

After you create a new set of Scenarios, it is always wise to save the Project so that you won't lose your Scenarios if something later goes wrong. (However, *VORTEX* always prompts you to save each open Project when you exit the program, so you do have a chance later to save everything – if nothing does go wrong.)

Deleting Scenarios from Your Project

If you have created Scenarios that you no longer want, you can delete them by hitting the "Delete Scenario" command at the top of the Input window. This will delete the current Scenario. A prompt will first warn you that you cannot recover from this action (other than by re-creating the Scenario again).

Reordering scenarios

After you add and delete Scenarios from your Project, you may find that the Scenarios are not listed in the order you would like them to have. *VORTEX* provides a Scenario Manager (Figure 39), which you access by clicking on the "re-order" command next to the dropdown list of Scenario names. The Scenario Manager lets you change the order of the Scenarios in your Project (moving them up or down in the indexed list). A feature not currently implemented will allow you also to specify that some Scenarios are to be considered to be grouped as "sub-scenarios" of others (moving them to higher or lower levels of a Scenario tree structure). The level at which a Scenario is placed, and the Scenario under which lower level Scenarios are nested, has little or no meaning other than to the Sensitivity Analysis utility that has not yet been implemented.

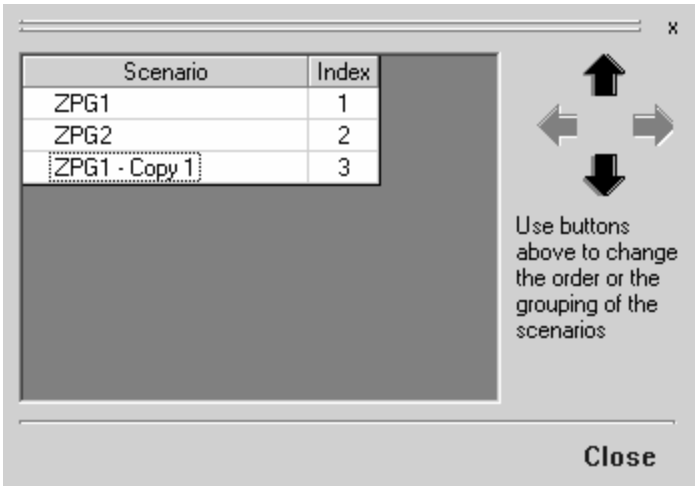


Figure 39. Scenario Manager window.

Chapter

4

Viewing Model Results: Text, Tabular, and Graphical Output

Once you have entered all of the necessary input parameters and given the command to run your first *VORTEX* model, you are ready to look at your simulation results. A display of changing population sizes was displayed (perhaps very quickly) on your screen as the simulation was running (Figure 36). While you may want to capture that image onto your Windows clipboard with a PrntScrn system command, the more useful presentations of model results are generally those that provide mean results across iterations, perhaps with standard deviations to indicate the variation among iterations or standard errors to indicate the precision with which the means were estimated from the finite number of iterations run. In addition, there are many measures of population performance and viability other than just the projected population size. This chapter describes how to use *VORTEX* to view text, tabular, and graphical summaries of your results.

Text Output

Click on the Text Output tab to access simple text descriptions of your Project input or results (Figure 40). There are four subsections of Text Output.

Input Summary

The first section provides a summary of the input values you entered for each Scenario. It is wise to scroll through this Input Summary in order to be sure that you entered the values as you intended. In addition, you can cut and paste from this text summary into any reports that you need to create of your work. At the top of the Input Summary, and similarly at the top of the other three sections of Text Output, are three command buttons. These allow you to send the text to the Project Report, print the text, or save the text as a file that you would specify. The Project Report will be described in detail later – it is a simple word processor that allows you to start building a report of your analyses while you are working within the *VORTEX* program. (You can then access that report from MS Word or other software to further edit and refine it.) If you chose to print the text, *VORTEX* will open the standard Windows Print utility. If you save the text, *VORTEX* saves it as a simple text file, which could later be viewed, edited, or printed from NotePad, MS Word, or other word processing software.

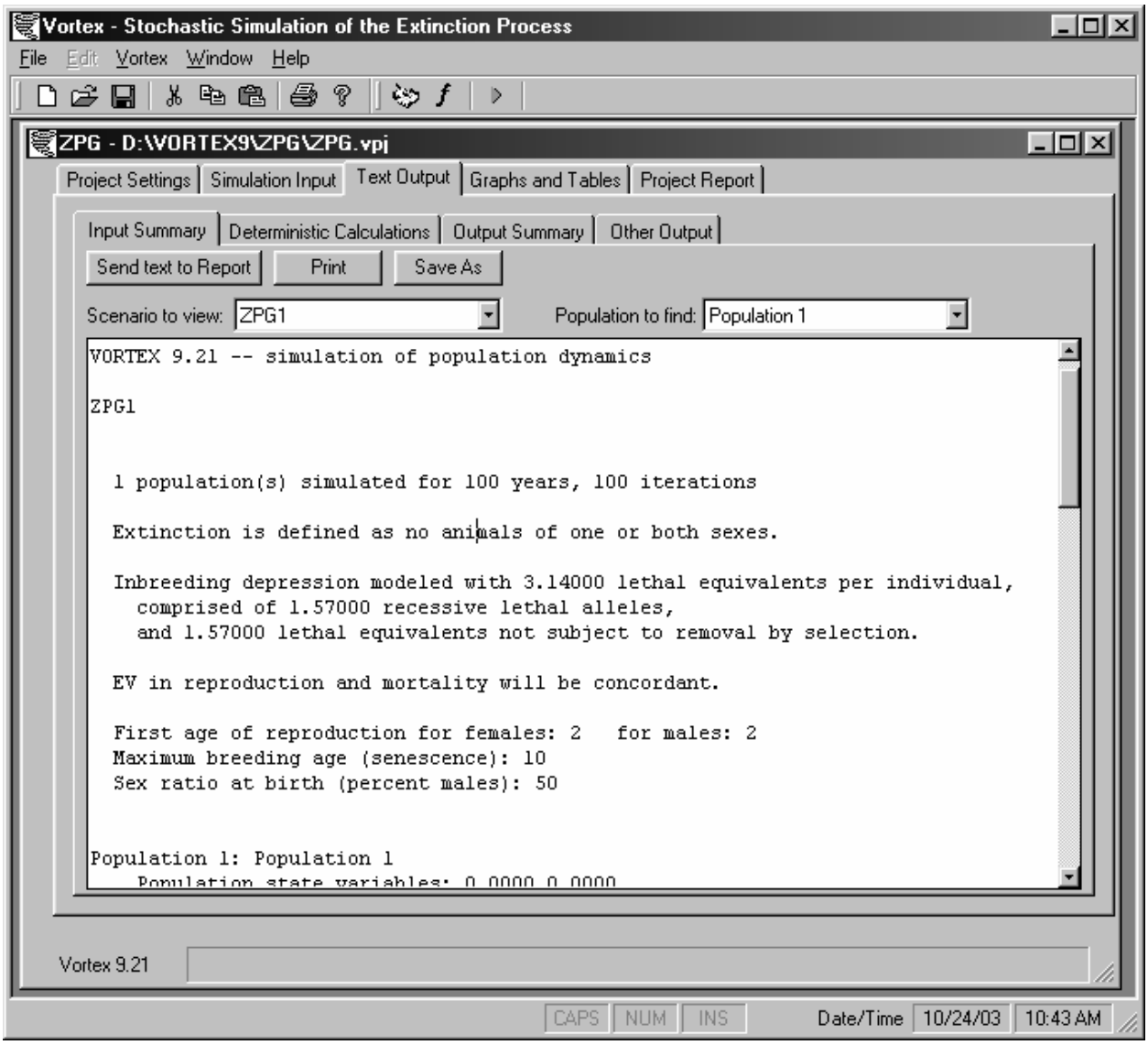

Vortex - Stochastic Simulation of the Extinction Process
File Edit Vortex Window Help
ZPG - D:\VORTEX9\ZPG\ZPG.vpj
Project Settings
Simulation Input
Text Output
Graphs and Tables
Project Report
Input Summary
Deterministic Calculations
Output Summary
Other Output
Send text to Report
Print
Save As
Scenario to view: ZPG1
Population to find: Population 1
VORTEX 9.21 -- simulation of population dynamics
ZPG1
1 population(s) simulated for 100 years, 100 iterations
Extinction is defined as no animals of one or both sexes.
Inbreeding depression modeled with 3.14000 lethal equivalents per individual,
comprised of 1.57000 recessive lethal alleles,
and 1.57000 lethal equivalents not subject to removal by selection.
EV in reproduction and mortality will be concordant.
First age of reproduction for females: 2 for males: 2
Maximum breeding age (senescence): 10
Sex ratio at birth (percent males): 50
Population 1: Population 1
Vortex 9.21
CAPS
NUM
INS
Date/Time
10/24/03
10:43 AM

Figure 40. Input Summary section of Text Output.

At the top of the text display window are dropdown lists that let you move among the reports for the various Scenarios and Populations (within Scenarios). In the Input Summary, all Populations in each Scenario are contained within the same text file, so you could find them by scrolling down. However, the file can be very large, so it is often faster to use the dropdown list to jump to the place where text on a Population starts.

Deterministic Calculations

The second section of Text Output provides both text and a simple graph to display the deterministic projections of population size (Figure 41). The text window shows the exponential rate of increase, r, the annual rate of change, λ, and the per generation rate of change or "net replacement rate", R0, as determined from life table analysis of the mean rates of reproduction and survival in your model. The mean generation time and a stable age distribution (calculated from age-specific birth and death rates) are

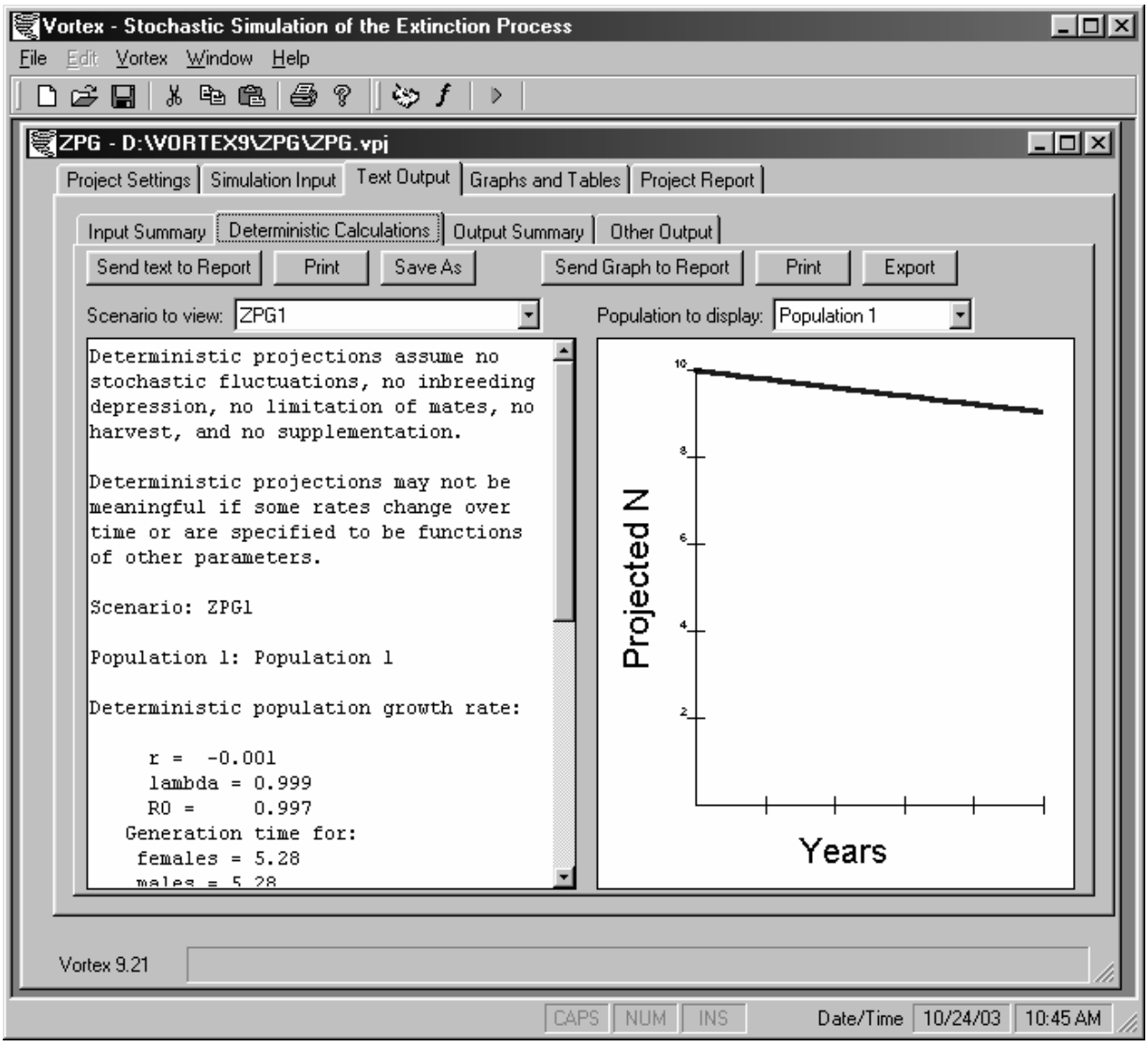


Figure 41. Deterministic Calculations shown in Text Output.

also given. See Box G for a brief description of these deterministic calculations.

The graph given with the Deterministic Calculations is fairly simple and crude, but it shows the exponential growth (or decline) projected from the life table calculations (up to the limit set by the carrying capacity). The graph can be sent to your Project Report, printed, or exported to a bitmap (.bmp) file for import into other programs.

The deterministic calculations are performed by *VORTEX* as soon as you enter the input values for your model. Therefore, you can view these results (and also the Input Summary text) even before you run your simulations. It is often helpful (and always recommended) to look at the deterministic projections before proceeding with stochastic simulations, so that you will know whether the rates of reproduction and survival are at least minimally adequate to allow for population growth in the absence of random fluctations and other destabilizing processes (such as inbreeding and harvest).

Box G: Deterministic Calculations in *VORTEX*

Before the actual stochastic simulation begins, *VORTEX* performs a standard life table analysis to calculate the deterministic mean population growth rate (r, the exponential growth rate; or λ ("lambda"), the annual multiplicative growth rate), the mean generation time for males and females, and the stable age distribution used (optionally) to initialize the starting population. These calculations will provide accurate long-term averages, if stochastic variation (due to demographic stochasticity, environmental variation, catastrophes, and inbreeding effects) is minimal. Life table analyses implicitly assume that age-specific birth and death rates are constant through time; they yield over-estimates of long-term population growth if there is any variation in demographic rates.

The deterministic population growth rate r is calculated by solving the Euler equation:

$$\sum\left(l_x m_x e^{-rx}\right)=1,$$

in which l_x and m_x are the age-specific mortality and fecundity rates, respectively for age class x to x+1, and the summation is over all age classes. Lambda is related to r by:

$$\lambda = e^{r}.$$

The stable age distribution, or the proportion of the population at each age class c_x, is given by:

$$c_x = \frac{l_x e^{-rx}}{\sum\left(l_x e^{-rx}\right)}.$$

The determination of a stable age distribution for males in a given population becomes a bit more complicated if the mortality schedules are different for the two sexes. In this case, r is calculated based on female life history tables (since females control population growth), but the l_x's used in the age distribution equation are those for males. Moreover, the exact form of the equation is dependent on when the age classes were censused. In the above equation, c_0 is the proportion of the population aged 0 plus a small increment, just after the breeding season but before mortality is imposed. In order to build the initial population, *VORTEX* omits age class 0 (because the simulations begin just before the breeding season), and re-scales the age distribution in order to sum to 1.0.

The life table calculations assume that there is no limitation of mates (i.e., there are always enough breeding males to mate with all breeding females). Other complications arise if there are catastrophes in the simulation model. In those cases, *VORTEX* adjusts the fecundity and mortality rates to account for the effect of catastrophes, averaged across years.

For more information on the details of life table analysis, refer to any number of general ecology or population biology texts such as Pielou (1977), Krebs (1994), or Caughley (1977).

It is important to look at the deterministic projections of population growth for any analysis. If r is negative, the population is in deterministic decline (the number of deaths outpace the number of births), and will become extinct even in the absence of any stochastic fluctuations. The difference between the deterministic population growth rate and the growth rate resulting from the simulation can give an indication of the importance of stochastic factors as threats to population persistence.

Output Summary

The third section of Text Output lists the basic status of each population at each year of the simulations.

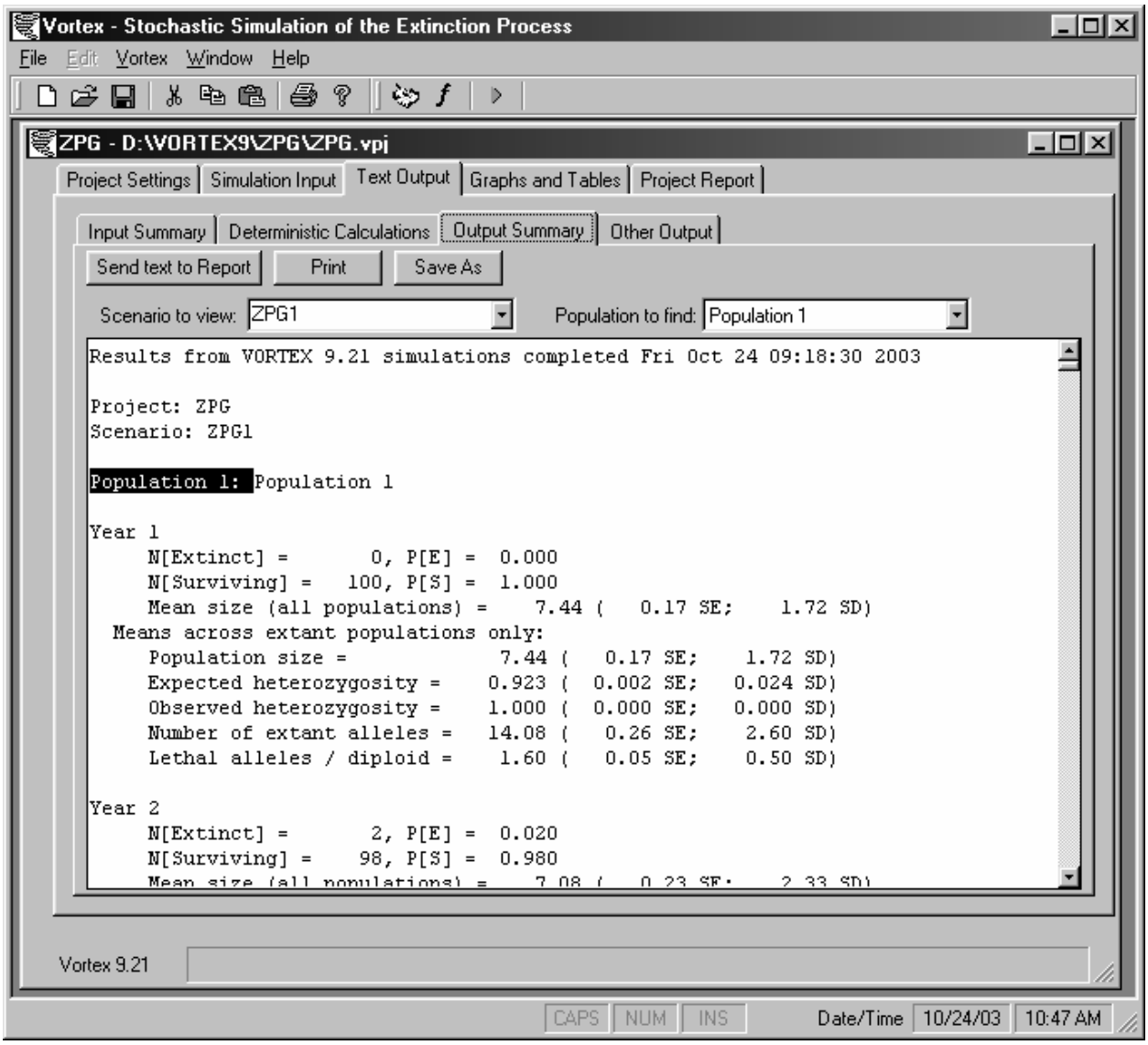

Vortex - Stochastic Simulation of the Extinction Process
File Edit Vortex Window Help
ZPG - D:\VORTEX9\ZPG\ZPG.vpj
Project Settings
Simulation Input
Text Output
Graphs and Tables
Project Report
Input Summary
Deterministic Calculations
Output Summary
Other Output
Send text to Report
Print
Save As
Scenario to view: ZPG1
Population to find: Population 1
Results from VORTEX 9.21 simulations completed Fri Oct 24 09:18:30 2003
Project: ZPG
Scenario: ZPG1
Population 1: Population 1
Year 1
N[Extinct] = 0, P[E] = 0.000
N[Surviving] = 100, P[S] = 1.000
Mean size (all populations) = 7.44 (0.17 SE; 1.72 SD)
Means across extant populations only:
Population size = 7.44 (0.17 SE; 1.72 SD)
Expected heterozygosity = 0.923 (0.002 SE; 0.024 SD)
Observed heterozygosity = 1.000 (0.000 SE; 0.000 SD)
Number of extant alleles = 14.08 (0.26 SE; 2.60 SD)
Lethal alleles / diploid = 1.60 (0.05 SE; 0.50 SD)
Year 2
N[Extinct] = 2, P[E] = 0.020
N[Surviving] = 98, P[S] = 0.980
Vortex 9.21
CAPS NUM INS Date/Time 10/24/03 10:47 AM

Figure 42. Output Summary section of Text Output.

The statistics reported in this file are:

- The cumulative number of iterations (populations) that have become extinct or remain extant;
- The probability of population extinction (PE) or survival (equivalent to the proportion of iterations (populations) that have become extinct or remain extant);
- The mean population size, reported separately for all populations (N-all) and only for those remaining extant (N-extant), with standard error (SE) and standard deviation (SD) across iterations;
- The mean stochastic growth rate (r), both with and without harvest or supplementation (if applicable) as well as across all years of the simulation;

- The mean "expected heterozygosity" (or "gene diversity") remaining in the extant populations, with standard error and standard deviation across iterations;
- The mean "observed heterozygosity" (equal to 1 – [mean inbreeding coefficient]) remaining in the extant populations, with standard error and standard deviation across iterations;
- The mean number of alleles remaining (AllelN) within extant populations (from an original number equal to twice the number of founder individuals), with standard error and standard deviation;

and, if the inbreeding depression option is included in the simulation,

- The number of lethal alleles remaining per diploid individual, with standard error and standard deviation, determined by the nature and extent of the genetic load identified in the input process, and the intensity of inbreeding the population undergoes.

Following these yearly reports, the output file presents a series of final summary information that includes:

- The final probability of population extinction and, the converse, the probability of population persistence;
- If at least 50% of the iterations went extinct, the median time to extinction;
- Of those iterations that suffer extinctions, the mean time to first population extinction, with SE and SD across iterations;
- The mean times to re-colonization and re-extinction of those simulations that went extinct;
- The mean final population size, with SE and SD across iterations, for all populations, including those that went extinct (e.g., had a final size of 0);
- The mean final population size for those iterations that do not become extinct, with SE and SD across iterations;
- The final age-sex composition of the extant populations; and
- The mean population growth rate, with SE and SD across iterations. When harvesting or supplementation are included in your model, *VORTEX* will report the mean population growth rate for years without harvest or supplementation, for years with harvest or supplementation, and averaged across all years.

Additional summary information will be provided when you have built a metapopulation model. For example, the output file will also include the same set of summary data for the global metapopulation, and will also present a set of within-population means. These means are unweighted averages across populations, while the standard deviations are means of the individual standard deviations of the populations. Population sizes and genetic metrics are averaged across only those populations that survived some simulations. Similarly, times to extinction, recolonization, and re-extinction are averaged across only those populations that had some extinctions. Finally, if any recolonization events occurred during the simulation, *VORTEX* will report the frequency of recolonization, the mean time to recolonization, and the frequency and mean time to population re-extinction if appropriate.

Also given for metapopulations will be some tables of genetic distances (and identities), with standard errors, to show the amount of genetic differentiation that existed between populations at the end of the simulations.

Other Output

The fourth section of Text Output provides two summary tables, in grid formats (Figure 43). One table provides a line of basic summary statistics for each Population of each Scenario that has been run. The summary statistics tabulated are the number of iterations (#Runs), the deterministic growth rate (det-r),

the mean stochastic growth rate (stoc-r) experienced in the simulations, the SD of the stochastic population growth [SD(r)], and final values (at the end of the simulation) for many of the descriptive statistics listed above in the Output Summary. If a Scenario has been run several times, then the table will show the results from these multiple sets of simulations. Comparing results across repeated sets of simulations can indicate whether the number of iterations was large enough to give results that are sufficiently stable (precise) for your purposes. (You can also get an indication of this by looking at the reported standard errors.)

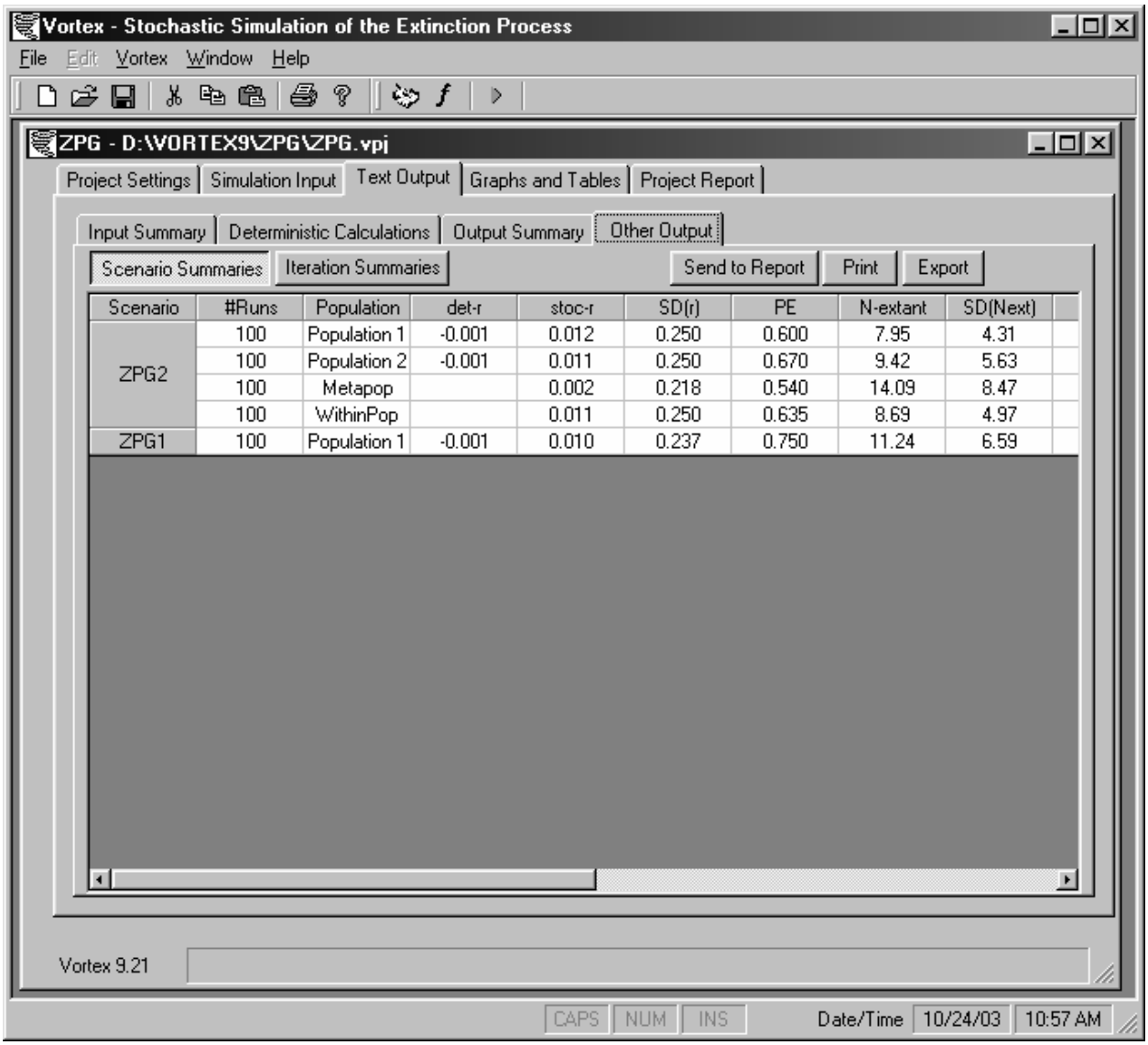

Vortex - Stochastic Simulation of the Extinction Process
File Edit Vortex Window Help
ZPG - D:\VORTEX9\ZPG\ZPG.vpj
Project Settings
Simulation Input
Text Output
Graphs and Tables
Project Report
Input Summary
Deterministic Calculations
Output Summary
Other Output
Scenario Summaries
Iteration Summaries
Send to Report
Print
Export
Scenario | #Runs | Population | det-r | stoc-r | SD(r) | PE | N-extant | SD(Next)
ZPG2 | 100 | Population 1 | -0.001 | 0.012 | 0.250 | 0.600 | 7.95 | 4.31
ZPG2 | 100 | Population 2 | -0.001 | 0.011 | 0.250 | 0.670 | 9.42 | 5.63
ZPG2 | 100 | Metapop | | 0.002 | 0.218 | 0.540 | 14.09 | 8.47
ZPG2 | 100 | WithinPop | | 0.011 | 0.250 | 0.635 | 8.69 | 4.97
ZPG1 | 100 | Population 1 | -0.001 | 0.010 | 0.237 | 0.750 | 11.24 | 6.59
Vortex 9.21
CAPS NUM INS Date/Time 10/24/03 10:57 AM

Figure 43. Scenario Summaries table in Other Output.

The other table in Other Output provides Iteration Summaries – a tabulation for each iteration of the year of extinction (if extinction occurs), final population size, and, if extinction does not occur, the final gene diversity, mean inbreeding coefficient, and number of founder alleles remaining. The data in this Iteration Summary table can be used to analyze the full distribution (not just the mean and SD) of the times to extinction, final population sizes, and genetic statistics. The "Export" button for the Other Output tables

will export these tables as text files delimited with semi-colons. These files can be imported directly into Excel or other spreadsheet software for further analysis (the column headers should transfer over).

Graphs and Tables

Click on the Graphs and Tables tab to access a section that lets you build tables and graphs displaying results for a variety of summary statistics (Figure 44). In the Data Specification tab of Graphs and Tables, you specify what Scenarios, Populations, Years, and Variables you want to put into the table that will be displayed at the right. *VORTEX* then also creates a graph of the data in your table, and gives you access to tools to customize your graph.

The Data Specification area can be confusing, but it gives you considerable flexibility in what you put into your tables and graphs. To understand how the Data Specification works, you should first realize that the results from your analyses can be considered to be a series of data points in a three-dimensional space.

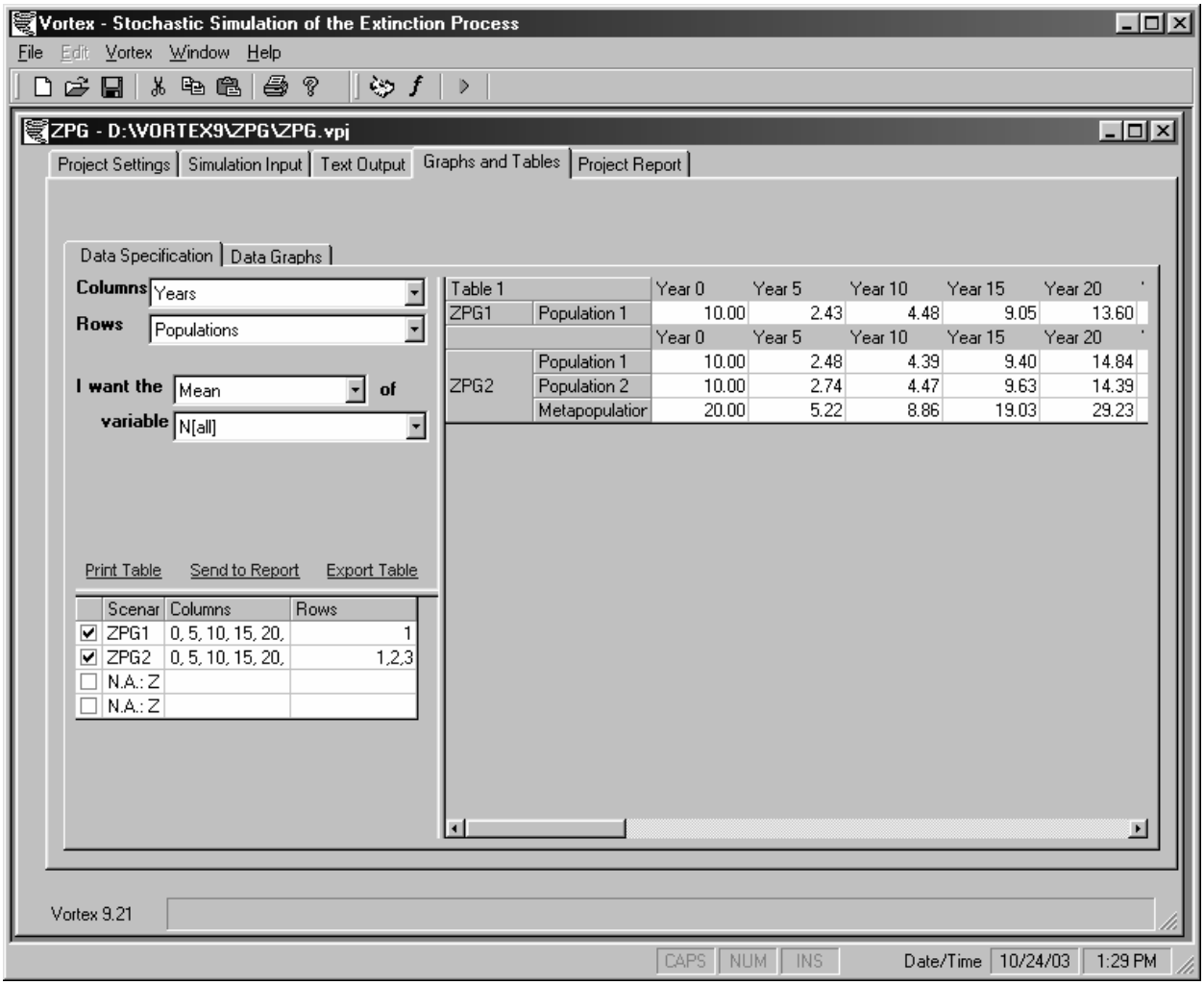

Vortex - Stochastic Simulation of the Extinction Process
File Edit Vortex Window Help
ZPG - D:\VORTEX9\ZPG\ZPG.vpj
Project Settings
Simulation Input
Text Output
Graphs and Tables
Project Report
Data Specification
Data Graphs
Columns Years
Rows Populations
I want the Mean of
variable N[all]
Print Table
Send to Report
Export Table
Scenar Columns Rows
ZPG1 0, 5, 10, 15, 20, 1
ZPG2 0, 5, 10, 15, 20, 1,2,3
N.A.: Z
N.A.: Z
Table 1 Year 0 Year 5 Year 10 Year 15 Year 20
ZPG1 Population 1 10.00 2.43 4.48 9.05 13.60
Year 0 Year 5 Year 10 Year 15 Year 20
ZPG2 Population 1 10.00 2.48 4.39 9.40 14.84
Population 2 10.00 2.74 4.47 9.63 14.39
Metapopulatior 20.00 5.22 8.86 19.03 29.23
Vortex 9.21
CAPS NUM INS Date/Time 10/24/03 1:29 PM

Figure 44. Data Specification and Table screen of the Graphs and Tables for output.

The three dimensions of the data are: Years (the year of the simulation at which the data point was taken), Populations/Scenarios (which Population from which Scenario is being observed), and Variables (which summary variable is being tabulated). These three dimensions need to be assigned to the columns, rows,

and cell values of the table you create. For example, a common table would be to display some Variable (such as the mean population size) as the cell contents, in a grid with a series of Years (such as 0, 10, 20, …) as the column headings and Populations (such as Population1, Population2, and Metapopulation) as the row headings. (See Figure 44 for an example of a table specification similar to this.)

However, you could instead want the Years to be arrayed down the side of the table as the rows, with the Populations across the top as the columns. To do this, you would select Populations from the dropdown list for Columns, and Years from the dropdown list for Rows. You could instead tabulate multiple Variables (such as PE, N, SD(N), and MedianTE) as columns with Populations as rows, or Variables as rows with Populations as columns. In the specification of the remaining dimension (Years) you then give from which Year of the simulation you want the value of these Variables displayed. (Usually, but not always, you would select the final year.) Figure 45 shows an example of a table of this type.

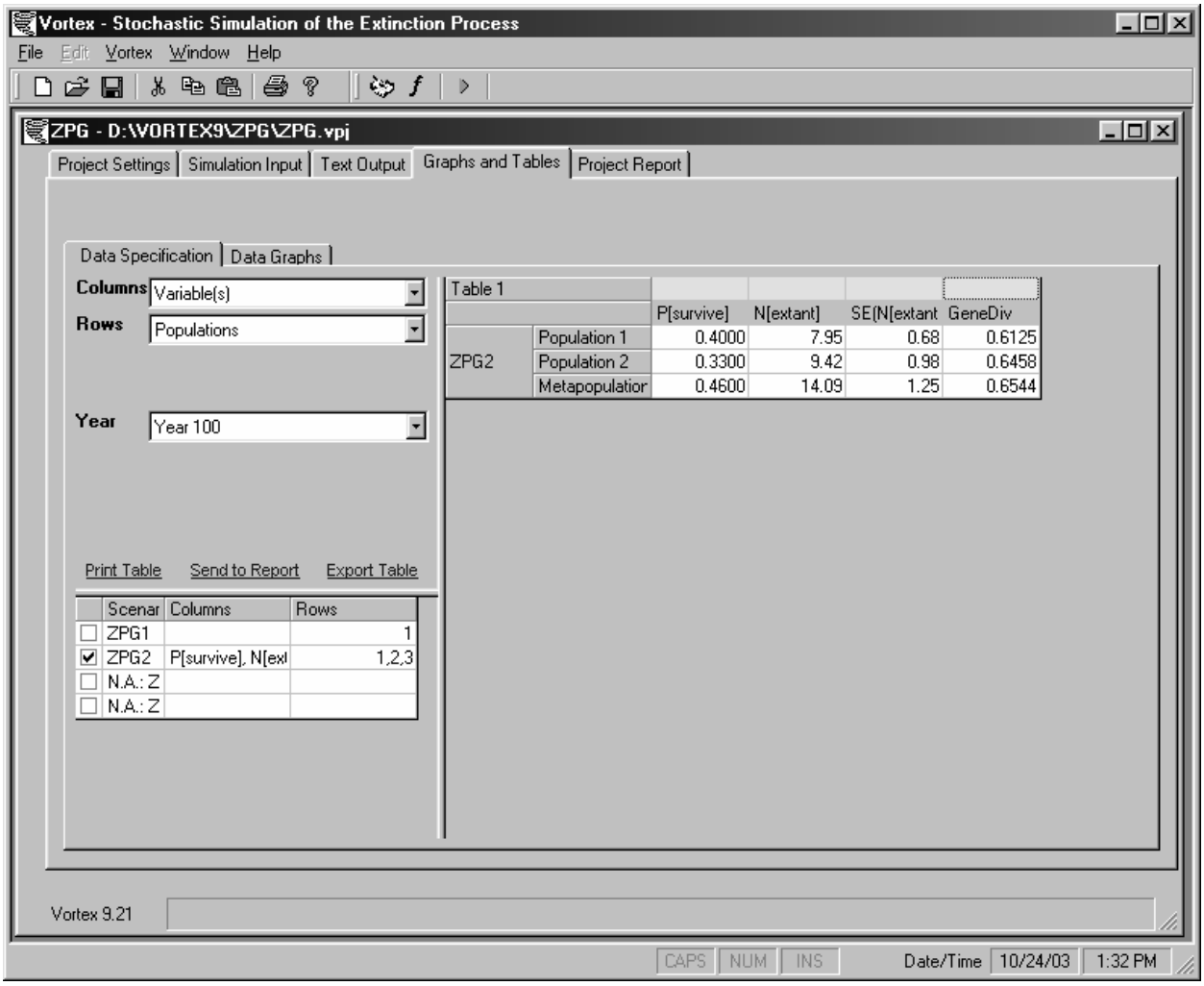


Figure 45. An example of a Table with Variables as Columns.

VORTEX can display a multi-part table, with results from a different Scenario shown in each part. You select which Scenario(s) you want to examine by checking the boxes in the grid on the lower left of the screen. To then specify which Years, Populations, and Variable(s) you want in your table, you need to specify the Columns and Rows in the grid in the lower left, and pick from the dropdown list which Variable/Year/Population is to be tabulated. The specification of Columns and Rows can be done by

typing the numbers of the desired Years or Populations into the grid under Columns or Rows, as appropriate.

Alternatively, you can click on the "…" button for Rows or Columns. That will open up a window for specification of the Years, Populations, or Variables, as appropriate (Figure 46).

Figure 46. Year Specification window for creating tables and graphs.

Specification of the Years in this window can be confusing, but it is also very fast once you learn how to use it. You can quickly "Select All" years by clicking on the command, if you want every year shown in your table and graph. (You can also "Deselect All" if you want to remove a prior selection.) To specify that only some years should be selected, you can check on those years in the grid. The boxes in the grid are arrayed across rows for each decade. That is, the check boxes in the first row of the grid are years 0, 1, 2, …, 9; the check boxes in the second row of the grid are years 10, 11, 12, …, 19; etc. If you want to select all of the years in one column (such as years 0, 10, 20, …), you can click on the column heading. Similarly, to select all of the years in one decade (e.g., 20, 21, 22, …, 29), you can click on the row label. The order in which you select the years is shown in the list that accumulates on the right, and this would be the order that the years show up in your data table. Presumably, you would want the years to be in ascending order in your table. To re-order the years, click on the "Sort Ascending" command. After you have selected (and possibly sorted) the years you want in your table, click "OK" to send that selection to the Data Specification screen.

Selection of Populations or Variables is done in a similar way, except that they are more straightforward to select because they are displayed in a single vertical list of check boxes.

After you have completed specification of your data table, you can click on commands to print the table, send it to your Project Report, or export it to a text file delimited with semi-colons.

Data Graphs

If you click on the Data Graphs tab, *VORTEX* will display a graph of the data that are in your table (Figure 47). The dimension used for table columns is plotted as the x-axis; the dimension used for the rows of the

table will create separate lines on the graph; the values displayed in the table will be the y-axis of the graph. To remember how the graph axes relate to the table lay-out, think of each row of the table as being plotted as a line on the graph, with the columns (place in the row) being the dependent (x-axis) variable and the value given in the table being the dependent (y-axis) variable.

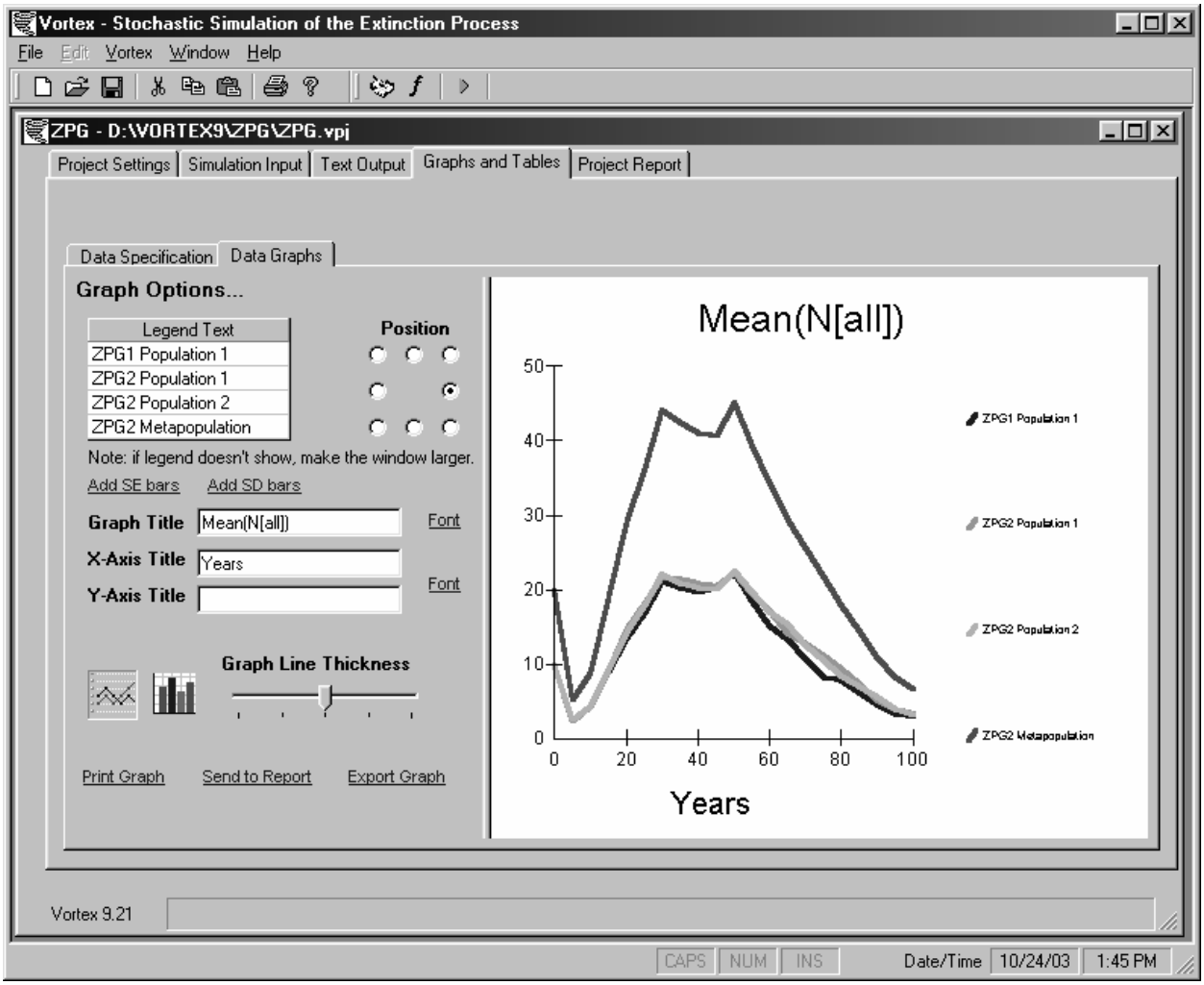


Figure 47. Data Graphs window.

The initial size of the Data Graphs window that opens up will often force your graph to be squeezed into a fairly small window, and often the legend will not be displayed (because it doesn't fit in the small window). To see a better image of the graph, click on the corner of the Project window and drag it out to a larger size.

On the Data Graphs window, you are provided with several Graph Options for changing the look of your graphs. You can change the text or position of the legend, the text or font of the main title or the axis titles, and the line thickness. You can also toggle between a line graph and a bar graph, although for many kinds of data that would be plotted only one of these two graphs would be reasonable. Command buttons are provided to allow you to Print the graph, send it to the Project Report, or Export the graph to a bitmap (.bmp) file. You can also add error bars to show standard errors (SE) around the plotted means, or standard deviations (SD) across iterations. The SE and SD options are available only for those plotted variables for which they would be applicable. (E.g., there is no error around deterministic growth rates.)

While these basic Graph Options will be adequate for many purposes, *VORTEX* also provides you with access to a much more extensive graphing utility. To fine-tune your graphs, right-click on the graph and select Properties. That will bring up an Advanced Graph Properties window that gives you considerable control over almost all aspects of the graph (Figure 48).

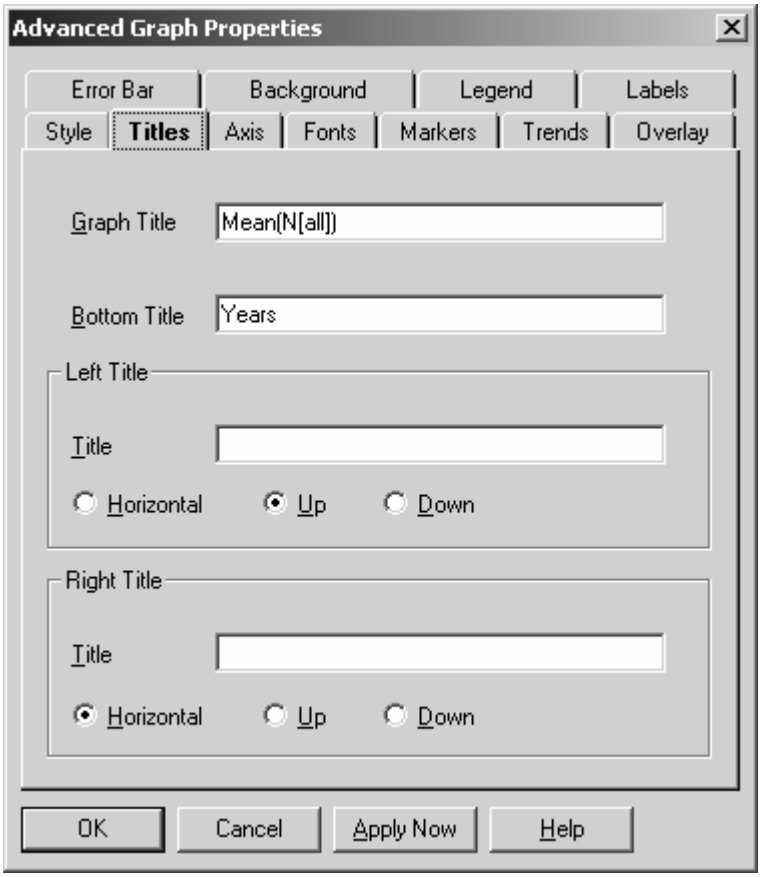


Figure 48. Advanced Graph Properties.

It is always good to watch the *VORTEX* website for upgrades! The Tables and Graphs section of *VORTEX* is still undergoing considerable improvements, as are many other sections!

Project Report

The Project Report tab takes you to a simple word processor utility that you can (and should) use to document your work and begin to develop a report for sharing with others (Figure 49).

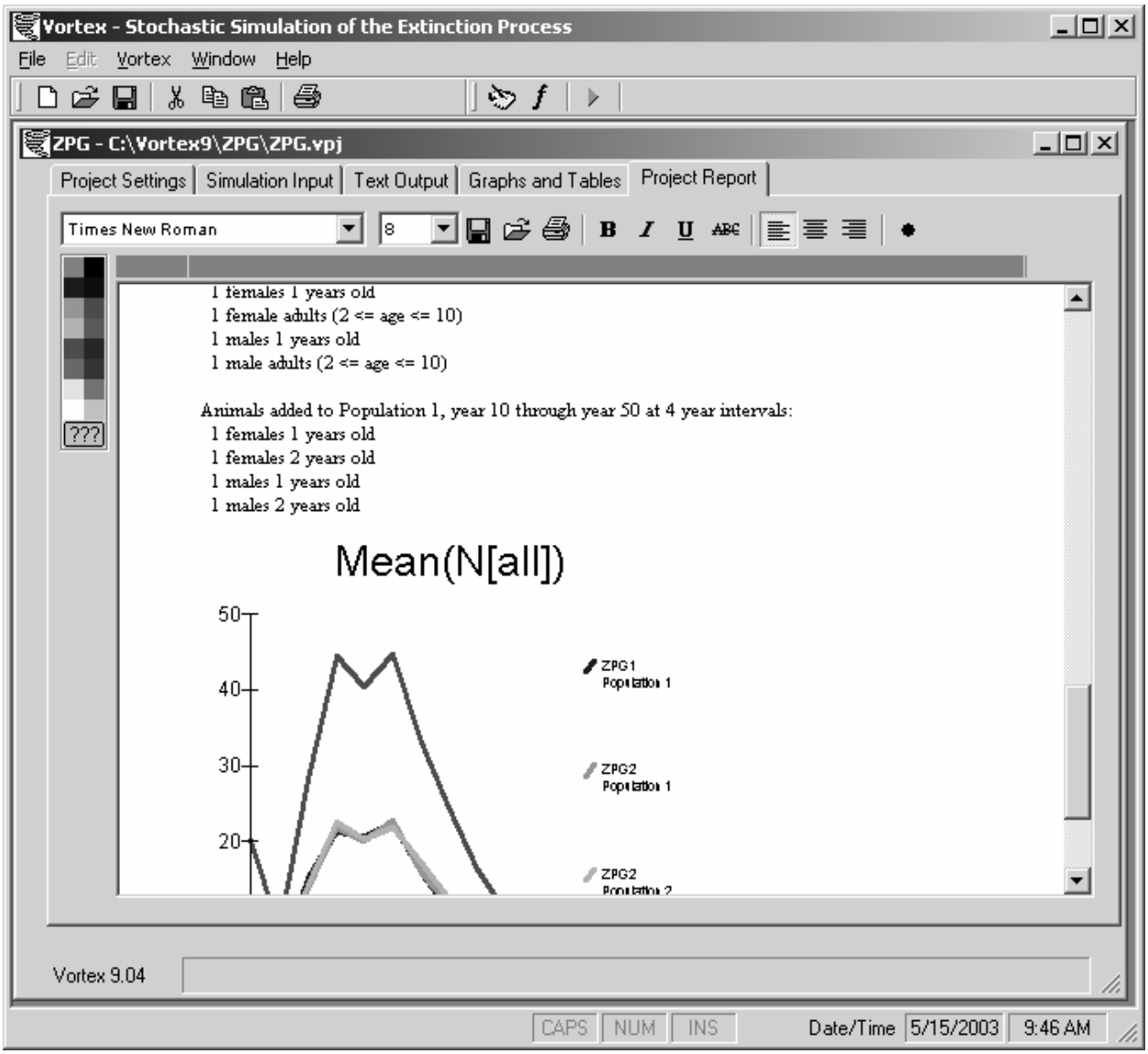


Figure 49. The Project Report.

In the earlier sections for Project Settings, Text Output, and Graphs and Tables, you had the option to send text, tables, and graphs to your Project Report. This is where you were sending them! It is always a good idea to liberally send information to your Project Report whenever you think that it may be information that you will want to capture for inclusion in project reports of any sort. It is always easy later to edit or delete sections of your Project Report, but it may be difficult to later resurrect information that you neglected to send to the report.

The Project Report gives you tools for standard format changes, including fonts, colors, italics, bold, alignment, and bullets. You also have the option to Save, Open, or Print reports. *VORTEX* automatically saves your Report with the Project, and re-loads it when you open the Project again. You only need to explicitly Save a Report if you wish to save it under a new filename. When you save a report, it is saved in Rich Text Format (an .rtf file). Such files can be imported directly into MS Word and most other word processors, where you can use their more powerful editing capabilities to further refine your report.

Access to Other Stored Output

The results made available to you in the Text Output and Tables and Graphs sections of *VORTEX* are all stored in text files (with extensions .inp, .det. .out, .dat, .sum, .run, and .rtf) placed into your Project directory. You can access these files directly if you wish to view the data within other word processing, spreadsheet, database, or graphical software. However, if you wish to edit these files in any way, you should first make a copy of the files and then edit only the copy. If you change the files that were created by *VORTEX*, you may make the data inaccessible when you re-open your Project. Another file that you should not edit is the file with extension .vpj. This "vortex project" file is the master file that stores the data for your Project. *Any changes made to this file outside of the VORTEX program can cause your Project to be corrupted and possibly un-openable.*

In addition to the results made available to you within *VORTEX*, the program stores other results in additional files that are placed into your Project directory. Some of these additional files contain more detailed results (often, far more detailed than most users would care to examine). These files typically are text files with semi-colon delimiters, formatted so that they can be opened directly into Excel and many other spreadsheet and database programs. Which additional files are created depends on the settings you select in the Special Options of the Project Settings. Available files include (in which "project" is replaced by the name of your Project, and "scenario" is replaced by the name of the Scenario):

project_scenario.run	A listing for each iteration of the year the population went extinct (if it did go extinct), and (if it did not go extinct) the final population size, gene diversity, mean inbreeding, and number of founder alleles.
project_scenario.ani	A listing for each iteration of the animals living at the end of the iteration, including their sex, age, inbreeding coefficient, and genotypes at the modeled loci.
project_scenario.gen	A listing of final allele frequencies and probabilities of allele persistence, averaged across the iterations, for the first locus modeled.
project_scenario_Iter#.gp	A listing in GenePop format of the individuals alive at the end of the iteration, including their sex, age, inbreeding coefficient, and genotypes at the modeled loci.

Chapter

5

Using Functions in *VORTEX*

Introduction

VORTEX provides the option of modeling demographic rates as functions of population or individual parameters. The population descriptors that can be used as variables in the functions include time (year in the simulation), iteration, population, population size, carrying capacity, numbers of juveniles (animals in the first age class), subadults (greater than 1 year, but not yet breeding age), adult females, adult males, all females, or all males, and gene diversity (expected heterozygosity). Individual characteristics that can be entered as variables in these functions include ID#, sex, age, number of mates (0 or 1 for females and monogamous males; possibly more for polygamous males), inbreeding coefficient, and genotypes at modeled loci. Almost all demographic rate parameters – such as the percent of females breeding each year, environmental variation in breeding, litter/clutch size, sex ratio, mortality rates, environmental variation in mortality, catastrophe frequency and severities, carrying capacity, dispersal, dispersal mortality, occurrence of harvest and supplementation, and definition of extinction – can be specified to be functions of the above population and individual variables.

The flexibility to specify population rates as functions rather than as fixed constants has been added to *VORTEX* so that users can model specific population dynamics that might be known to be appropriate for some species, or that are of interest in a theoretical analysis. With some creativity and perhaps considerable effort, *VORTEX* can now model many of the kinds of population dynamics that can be envisioned. As just a few examples:

- it might be known that carrying capacity will change at some determined date in the future;
- it might be believed that reproductive rates will change over time, perhaps due to some management action;
- the density dependence observed in reproduction might not fit the shapes of the curves allowed in previous versions of *VORTEX*;
- mortality rates might change over time, or respond in a complex way to population density;
- inbreeding might impact fecundity, adult survival, or might affect the two sexes differently;
- dispersal might be age and sex dependent;
- fecundity, mortality, or the effects of catastrophes might be age-dependent;
- environmental variation might occur with a periodicity that is longer than a year, or catastrophes might have multi-year effects.

Note that *VORTEX* includes within the basic data entry screens the option to model reproduction as a density dependent function, and an option to model carrying capacity as having a linear change over a

specified number of years. Easy access to these two particular functions are provided because they are needed more frequently than are detailed functional dependencies of most other rates. Even for these two rates, however, you can specify these functions to have almost any shape if you use the function editor to specify the rates.

For most users and for most purposes there will be no need or desire to model demographic rates as functions; it is usually fully adequate to specify fixed demographic rates rather than functions. Specification of rates as functions can be difficult: the appropriate form of the function is rarely known, the function parameters are usually very difficult to estimate, and it is not trivial to enter a function correctly. If alternative functions need to be examined in sensitivity testing, the number of combinations of input parameters to be explored can quickly become overwhelming. Consequently, we would not recommend that novice users or students use the function option within *VORTEX*.

Specification of Demographic Rates as Functions

Dependencies of demographic rates on population and individual parameters are entered into *VORTEX* by specifying the functional relationships. There are two ways that you can enter a function rather than a constant for an input variable: you can type the function directly into the input box for specifying the rate, or you can open a Function Editor to help you develop the function to describe the relationship. *VORTEX* provides an option (and this option is the default for new Projects) to have the Function Editor open automatically whenever you enter a "=" as the first character in an input box for a demographic rate. The other way to open the Function Editor is to click on the Function Editor icon on the toolbar. If you type a function directly into an input box, you must precede the function with an "=" sign (to distinguish the specification of a rate as a function rather than as a constant). If you open the Function Editor by typing an "=" in an input box, and then develop a function within the Function Editor, then the Function Editor will insert the function back into the active input box when you accept the function. It is usually easier (and safer) to build a function first within the Function Editor and then send it over to the input screen.

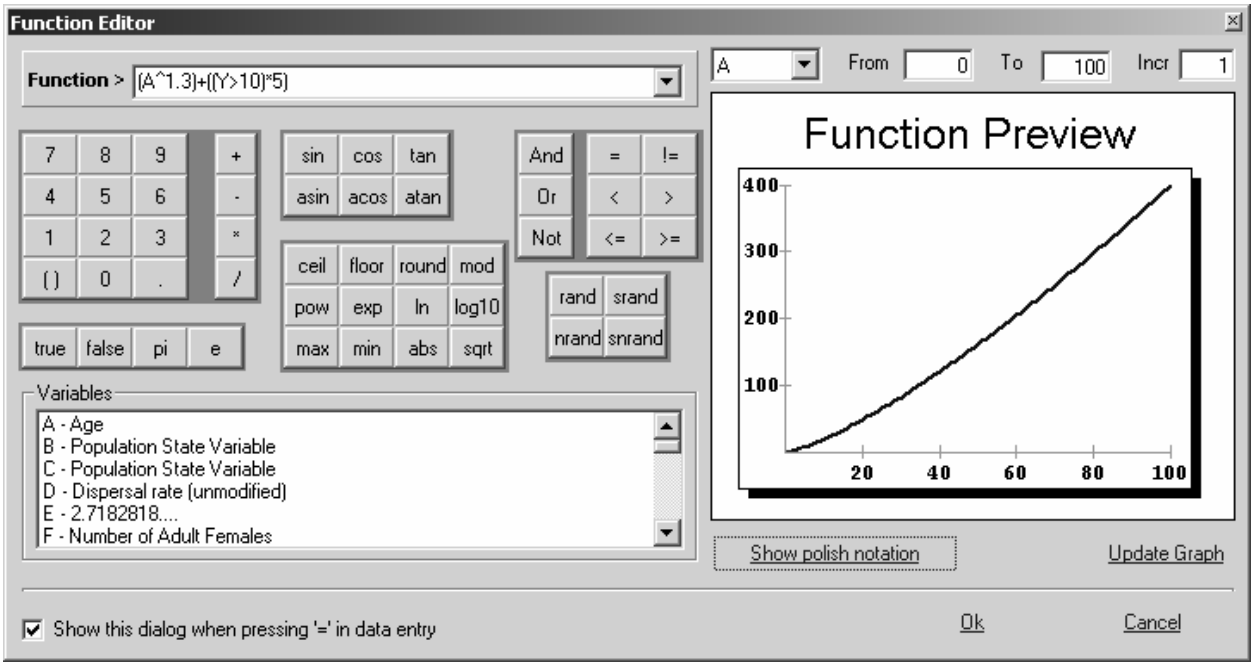


Figure 50. The Function Editor utility.

When you open the Function Editor (Figure 50), you can enter the desired function by typing it into the box at the top of the window, or you can use the screen keypads to select numbers, operators, and functions, which will then be pasted into the function box. It is probably fastest to just type the function you want, but the keypads can help remind you what operators, trigonometric functions, Boolean operators, and other functions are available for use. The population and individual variables available for use in functions are listed in a box in the lower part of the Function Editor window (see Table 1). The Function Editor also keeps a list of recently used functions, and they can be recalled (and further edited, if desired) by clicking of the drop-down list in the Function box.

In specifying a function, you should make no assumptions about the order of precedence of operators (see Table 2 for list of valid operators). For example, the function A+B*C is interpreted as (A+B)*C. (Precedence is left to right, so *VORTEX* interprets A*B+C in the standard way, but it is risky to assume that *VORTEX* will read a function the way you would read it.) *Always use parentheses to specify the order in which operations are to be performed.* (Parentheses), [brackets], and {braces} may be used interchangeably to indicate the order of operations.

Functions cannot contain any spaces or extraneous punctuation. Case of function names and variables is ignored. All letters that are entered in a function within the Function Editor are converted to upper case by *VORTEX*.

It can be difficult to correctly specify the function that describes the relationship you want for a demographic rate. To help you confirm that you have specified the correct function, *VORTEX* can display a simple x-y Function Preview plot of any function entered into the Function Editor. From the drop-down list above the graph, you must select which dependent variable from your function should be plotted along the x-axis. The plot will show the relationship to the selected x-variable, with each other dependent variable fixed at some simple value (e.g., sex = female, K = 100, N = 100, numbers of males, females, juveniles, and subadults = 50, iteration = 1, year = 1, population = 1, gene diversity = 100%, inbreeding = 0). You can change the range and increment of the x-axis if you wish. The Function Preview graph will not display until you click the "Update Graph" command.

If you know how to read reverse Polish notation for functions, you can click the command to "Show Polish Notation" in order to confirm that *VORTEX* is interpreting the parentheses to produce the order of operations that you desired.

After you have confirmed that you have the function that you want, you can cut and paste it into an input box, or (if you triggered the Function Editor by typing an '=' into an input box) just hit 'OK' to transfer your function over to the input box you had left.

Table 1. Valid Function Variables

Population descriptors

- **N** = Population size
- **K** = Carrying capacity
- **Y** = Year
- **P** = Population identifier
- **R** = Run (simulation iteration)
- **M** = Number of adult males in the population
- **F** = Number adult females
- **J** = Number of juveniles (age 0-1)
- **U** = Number of subadults (age > 1, < breeding age)
- **X** = Number of females (all ages)
- **W** = Number of males (all ages)
- **G** = Percentage of initial gene diversity (expected heterozygosity) remaining in the population
- **B and C** = population state variables (entered with population labels)
- **D** = Dispersal rate (from the matrix entered), used only in functions modifying dispersal.

BB(p), CC(p), etc. = the parameter above (**B, C,** etc.) for population **p**.

Individual descriptors

- **A** = Age
- **O** = Individual ID (an arbitrary integer assigned to each individual)
- **S** = Sex (0 or 'F' for female, 1 or 'M' for male)
- **I** = Inbreeding coefficient (must be expressed as a percentage)
- **Q** = Number of mates (0 or 1 for females and monogamous males, possibly more for polygamous males)
- **V** = Paternal allele identifier
- **Z** = Maternal allele identifier

VV(i) and ZZ(i) = the paternal and maternal alleles at the **i**th modeled locus.
IS1, IS2, IS3, … , IS9 = Individual State Variables previously defined.

Table 2. Valid Operators *(Note that there are alternative names for several operators.)*

Function	Description	Example
Unary Operators		
ABS	Absolute value	ABS(-10) = 10
NEG	Negative	NEG(-10) = 10
CEIL	Ceiling	CEIL(3.12) = 4
FLOOR	Truncate	FLOOR(3.12) = 3
ROUND	Round	ROUND(3.12) = 3 ; ROUND(5.5) = 6
SQRT, SQR	Square root	SQR(1.44) = 1.2
LN, LOG	Natural logarithm	LN(1.60) = 0.47
LOG10	Base 10 logarithm	LOG10(1.60) = 0.20412
EXP	e raised to specified power	EXP(0.47) = 1.60
Binary Operators		
+	Addition	1.0+2.0 = 3.0
-	Subtraction	2.0-1.0 = 1.0
*	Multiplication	2.0*3.0 = 6.0
/	Division	6.0/2.0 = 3.0
POW, ^	Exponentiation	POW(10,0.20412) = 10^0.20412 = 1.60
MAX	Maximum	MAX(3.12,4.21) = 4.21
MIN	Minimum	MIN(3.12,4.21) = 3.12
MOD, %	Modulus (Division remainder)	MOD(33,10) = 33%10 = 3; MOD(33.5,5) = 3.5
Logical (Boolean) Operators		
==, =	Is equal to	(3=2) = 0 = FALSE
NOT, !	Negation	!(3=4) = 1 = TRUE
!=, #	Not equal to	(3#4) = 1
AND, &&	And	((3=4)AND(3#4)) = 0
OR, ||	Or	((3=4)OR(3#4)) = 1
>	Greater than	(3>4) = 0
<	Less than	(3<4) = 1
>=	Greater than or equal to	(3>=3) = 1
<=	Less than or equal to	(3<=3) = 1
Trigonometric Operators		
SIN	Sine	SIN(PI/2) = 1.0
COS	Cosine	COS(PI/2) = 0.0
TAN	Tangent	TAN(PI/4) = 1.0
ASIN	Arcsine	ASIN(1.0) = 1.5707963
ACOS	Arccosine	ACOS(0.0) = 1.5707963
ATAN	Arctangent	ATAN(1.0) = 0.7853981
Defined Constants		
PI	3.1415927	SIN(PI/4) = 0.7071067
E	2.7182818	LN(E) = 1.0
TRUE	1	(10>5) = TRUE
FALSE	0	!TRUE = FALSE
Random Number Generators		
RAND	Uniform random (0 – 1)	RAND = 0.2341 or 0.8714 or 0.9151 or …
NRAND	Normal random deviate	NRAND = 0.512 or -0.716 or -2.376 or …
SRAND	A "seeded" random number generator; hence, SRAND(x) provides a random number between 0 and 1 with a given seed value x	
SNRAND	A "seeded" random normal deviate; hence, SNRAND(x) returns a number from a (0,1) normal distribution with the seed value x	

Using Random Numbers in Functions

Random number generators can be used to create a wide variety of stochastic events (for example, a 5--year drought that occurs on average once every 30 years), but the proper use of these functions requires careful consideration of how the "seed" values (implicit, as in **RAND** and **NRAND**, or explicit, as in **SRAND** and **SNRAND**) determine when new random numbers are selected. Repeated calls to the random number return the same value if the same seed is specified. Random numbers produced with different, even sequential, seeds will not be correlated. The "unseeded" forms (**RAND** and **NRAND**) set their own unique (or nearly so) seed each time they are called. The very first use of a random number generator in *VORTEX* uses a seed based on the number of seconds elapsed since the turn of the century. Each call to an unseeded random number generator also sets a new seed for the next call for an unseeded random number. Thus, two identically configured computers starting the same simulation at exactly the same second on their clocks would produce identical results for an analysis. This synchrony may require, however, that all memory storage locations (including hard disk caches) and even the hard disk contents are identical on the two systems (because they will affect the time required for each read or write to the disk).

The specification of random number seeds allows synchronization of sequences of random numbers. This can be used to create synchrony of events, such as catastrophes or environmental variation across populations, or autocorrelations among years (time lags or cycles). If several different demographic rates are specified by functions containing random number generators (perhaps to trigger separate catastrophes impacting survival and fecundity), care must be taken to create the desired synchrony or lack of synchrony. If two functions contain the same seed values, they will return the same random number. Seed values must be distinct to create independence of random numbers. (See examples below.)

Proper use of random number seeds can be difficult. Think carefully about the effect of any seed that you use in a function, to be certain that it will produce the same random numbers when you want them, and independent random numbers otherwise. Any variable (e.g., **A** for age, **Y** for year, **R** for run, **P** for population) included within the seed will cause the same "random" number to be chosen for each case with the same value for those variables (**A**, **Y**, **R**, **P**). For example, if you specify **SRAND(P)** within a function, then each population will get an independent random number, and that set of random numbers will be the same over all calls to evaluate that function (such as for every year, every run, and every individual within each population). If you specify **SRAND((P*100)+Y)**, then each population will get a new independent random number each year of the simulation, but the set of random numbers will be the same across all runs of the simulation. You would normally want to include the variable **R** in the random number seeds (e.g., **SRAND((R*10000)+(P*100)+Y)**), in order to cause the random numbers to be independent among runs of the simulation. See the examples below for further information about random number seeds.

The seeds used by *VORTEX* will be converted to integers between 0 and 65536. Non-integer seeds will be truncated [hence, **SRAND (35.23) = SRAND(35.89)**] and values above 64K will be "wrapped" [the modulus taken, so that **SRAND(65636)** = **SRAND(100)**].

Notes Regarding Function Syntax and Use

- Variables of trigonometric functions are assumed to be in radians.
- The operator **NEG** is the same as using a minus (-) sign before a number. By the context, *VORTEX* will interpret whether a minus sign signifies subtraction (a binary operation) or the negative (a unary operation).

- CEIL, FLOOR, and ROUND convert real numbers to integer values, but all expressions are evaluated as real numbers. For example,
  `FLOOR(3.7)/FLOOR(4.1) = CEIL(2.1)/CEIL(3.7) = ROUND(3.1)/ROUND(3.6) = 0.75.`
- Numbers may be written with or without leading and trailing zeroes. Decimal points for integral values are optional. For example, all of the following are valid expressions: `3, 3.00, 0.03, .03, -0.30, -5`.
- Functions containing invalid mathematical expressions are prohibited, such as:

`SQR(-10)`	Square root of a negative number
`LN(-10)`	Natural log of a negative number or zero
`5/0`	Division by zero
`TAN(1.5707963)`	Tangent of PI / 2
`ASIN(1.1)`	Arcsine or arccosine of a value greater than 1 or less than –1

- Some mathematically valid functions would be ambiguous or meaningless. For example, functions of carrying capacity (`K`) should not contain `K` as an independent predictor (of itself). Functions of `K` should also not include `A` (age) or `S` (sex) as parameters, because the condition of exceeding the carrying capacity is a population-level phenomenon, and `K` is assessed once for each population each year. If `K` is a function of inbreeding (`I`), the value of `I` applied in the function will be the mean for the population.
- The total length of a function cannot exceed 512 characters. Functions cannot contain more than 24 numerical constants, or more than a total of 128 constants plus variables plus operators. (Often you can find an alternative form that is shorter.)
- Many of the variables that can be used in rate functions will themselves change during each year of the simulation. In order to avoid unresolvable interdependencies of parameters and rates, the population size (`N`) and sizes of subsets (`J`, `F`, `M`, `U`, `X`, `W`) and gene diversity (`G`) used in function evaluations are the numbers that were tallied at the last (pre-breeding season) census.
- Even without specifying rates as functions, many of the rates used in *VORTEX* can be specified to be different for different years, sexes, ages, or inbreeding levels. (e.g., age-specific mortality, inbreeding depression in juvenile mortality, linear trends in K, etc.) Be aware that the effects of any functions entered are imposed on top of such dependencies that might be given in the standard input format. For example, EV in carrying capacity could be specified via standard input, or via a function of the type
  `K = 100+(10*NRAND)`,
  thereby giving an annual level of EV in K equal to a standard deviation of 10. The advantage of creating EV by specification within functions (rather than more simply as a parameter given to *VORTEX*) is that you have greater control over how EV is implemented in the model. For example, it is possible to specify that EV is concordant between two populations (but not with others):
  `RATE = 50+[10*SNRAND(Y+(R*100)+[(P>2)*100*SRAND(P)])].`
  In this function, the overall mean demographic rate is 50 with annual fluctuations due to EV (SD) equal to 10. Populations 3 and greater will experience independent annual fluctuations, while populations 1 and 2 will fluctuate synchronously. The use of year (`Y`) in the seed for the random number causes a new random number to be used each year. The use of `R` (iteration or run) in the seed causes the sequence of seed values to be different in each simulation. The inclusion of `(P>2)*100*SRAND(P)` within the seed causes a different sequence of random numbers to be chosen for each population after the first two have been evaluated. The seeds must include `Y+(R*100)` to ensure that every year-iteration is independent. (If you use `Y+R` as the seed, then year 3 of iteration 1 will have the same value as year 2 of iteration 2, etc.) In the simpler example of EV in K given above, no seed was needed or specified, so an independent random number will be selected each iteration, each year, and each population. These examples show how elaborate and

non-intuitive the functions can become when you want to create even moderately complex models of population dynamics.

Using Functions to Examine Genetic Evolution

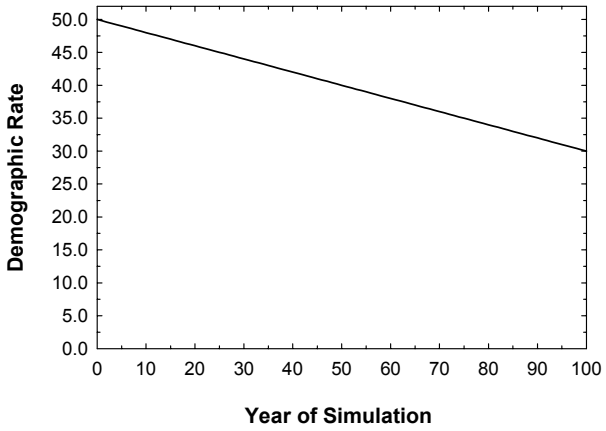
The parameters available for use in functions defining demographic rates include an individual's paternally inherited allele (**V**) and the maternally inherited allele (**Z**) of the (normally) non-selected locus, which is monitored for tracking genetic diversity. (The symbols for these variables **V** and **Z** have no intuitive meaning, but are rather the result of few letters remaining available for denoting additional parameters for functions.) By specifying that demographic rates are functions of the alleles carried by an individual, it is possible to model a wide variety of genetic processes impacting population dynamics, including: the effect and fate of alleles that confer alternative life history strategies (e.g., lower fecundity but higher survival); balancing, disruptive, or directional selection for alleles impacting demography; hybrid vigor or outbreeding depression caused by introgression of alleles from a distinct taxon or geographic population; and genetically based individual variation in demographic rates.

When the initial population is created, and when the population is supplemented with any new individuals, the founders are assigned unique alleles sequentially. Hence the first individual of the Population 1 is assigned alleles 1 and 2, the second individual is assigned alleles 3 and 4, and so on. Final frequencies of all founder alleles in each population, averaged across all iterations, can be outputed to a file if that option is selected within Special Options of Project Settings. The allele frequencies are placed into a file with extension **.gen**.

Examples of Rate Functions

The easiest way to demonstrate the formats in which functions can be entered into *VORTEX* is with a series of examples. The examples shown below include a plot of the function where appropriate as well as the actual expression.

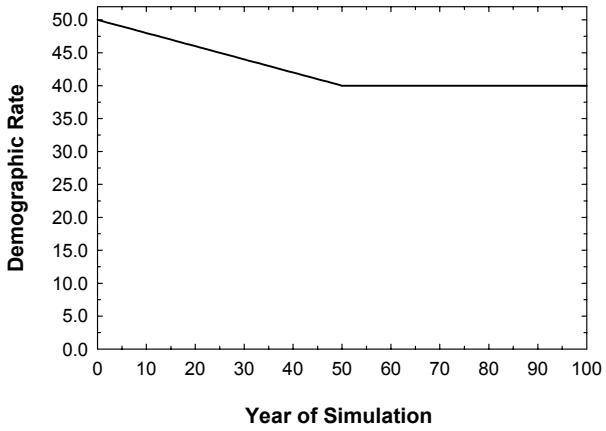
1. **Continuous linear decline over time**
   `RATE = 50-(0.2*Y)`
   This function specifies a starting rate (perhaps for adult female breeding success or for carrying capacity) equal to 50 in year 0, with a decline of 0.2 per year resulting in a rate equal to 30 after 100 years.



2. Linear decline limited to a period of years

```
RATE = 50-(0.2*MIN((Y-1),50))
```

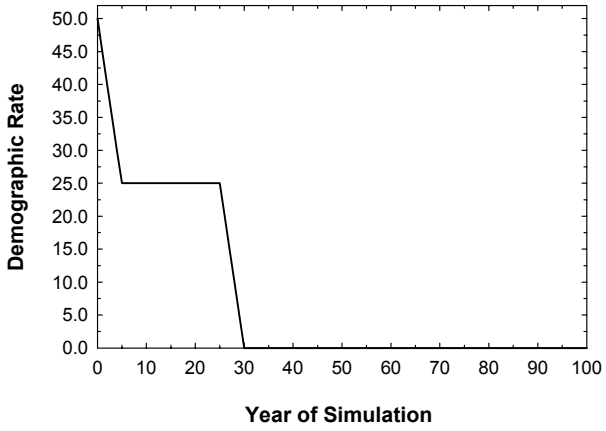
In this case, the decline occurs only through the first 50 years of the simulation. Note that the decline is specified to start in year 2, so that year 1 still has a rate of 50. This is the form of the function used by *VORTEX* if the user specifies a linear trend in carrying capacity.



3. Linear decrease during intervals of years

```
RATE = 50-(5*(MIN(5,Y)+((Y-25)*(Y>25))))
```

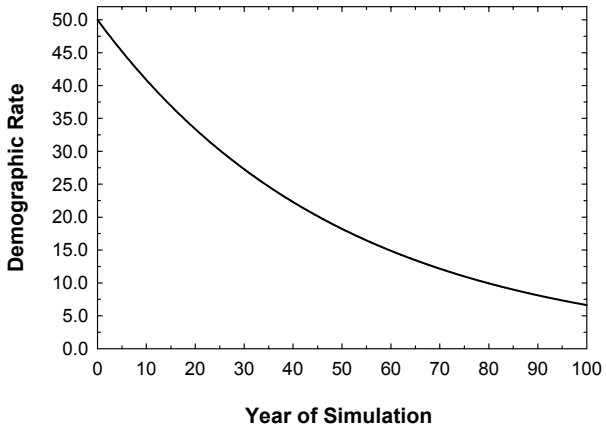
The rate starts at 45 in year 1, declines to 25 by year 5, and again resumes the decline at a rate of 5 per year after year 25.



4. Exponential decline

```
RATE = 50*(0.98^Y)
```

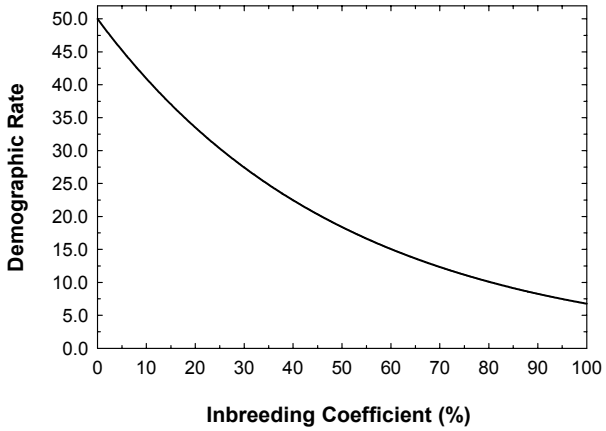
The rate declines by 2% each year.



5. Exponential decline with inbreeding

```
RATE = 50*EXP(-2.0*(I/100))
```

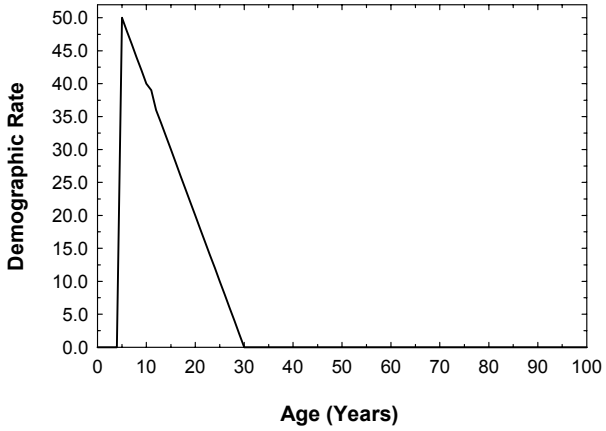
The rate declines from 50 in non-inbred animals down to 6.7 in fully inbred animals (I = 100%). Note that the inbreeding coefficient (**I**) is expressed as a percent. An equation like this might be used to specify a decline in fecundity due to inbreeding.



6. Age-dependent fecundity, with linear decline after the onset of breeding

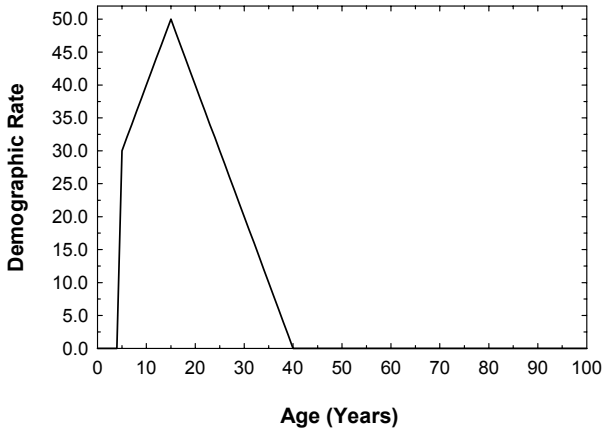
```
RATE = (A>=5)*(50-((A-5)*2))
```

Breeding begins with a rate of 50 at age 5, but then declines by 2 each year thereafter.



7. Age-dependent fecundity, with a symmetrical peak at age 15

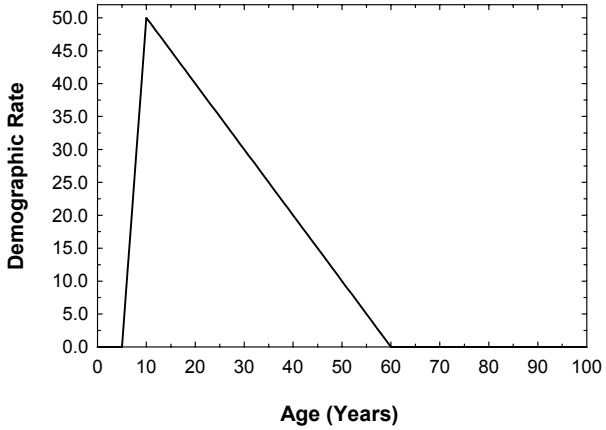
```
RATE = (A>=5)*(50-(ABS(A-15)*2))
```



8. Age-dependent fecundity, with an asymmetrical peak at age 10

```
RATE = (A>=5)*[{[A<10]*([A-5]*10)}+([A>9]*[60-A])]
```

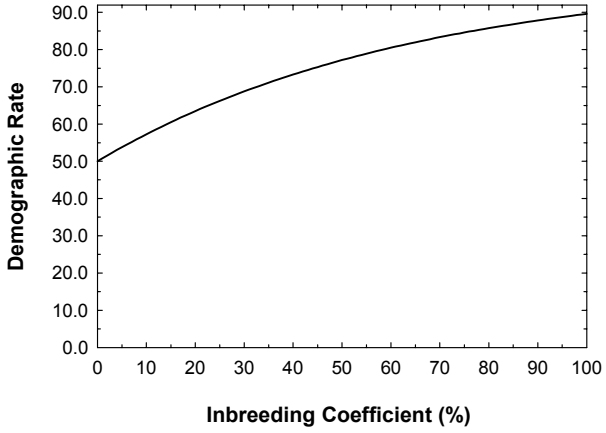
Different trends are specified for age intervals 0-4, 5-9, and 10+. Note the use of parentheses, brackets, and braces to improve readability.



9. Increase in mortality with inbreeding

```
RATE = 100-(50*EXP(-1.57*(I/100)))
```

The survival rate declines exponentially (described by the portion within the outermost parentheses), while the percent mortality is set at 100-survival. This is the equation used by *VORTEX* to model increased juvenile mortality if there are 3.14 lethal equivalents and no recessive lethal alleles contributing to inbreeding depression.

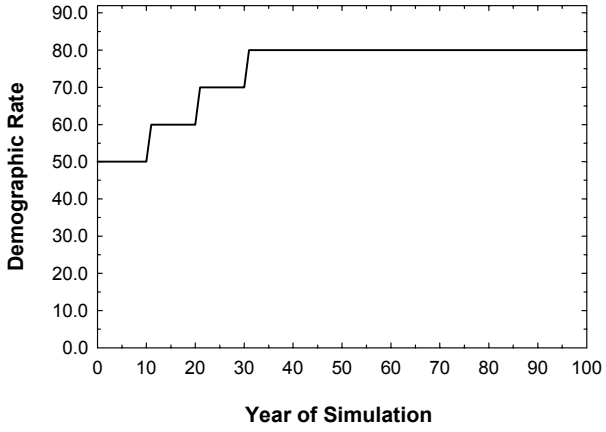


10. Stepwise increase

```
RATE = 10+((Y>10)*10)+((Y>20)*10)+((Y>30)*10)
```

The rate increases from 50 to 80 at 10-year intervals. An alternative way to express the same function would be

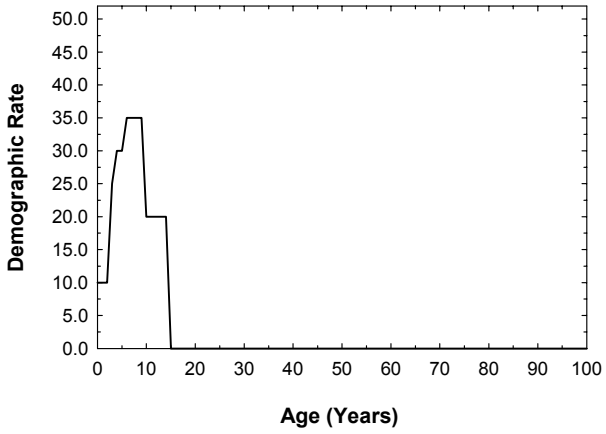
```
RATE = 50+(10*(MIN(3,FLOOR(
(Y-1)/10))))
```



11. Different rates at different intervals

```
RATE = (10*(A<3))+(25*(A=3))+(30*((A=4)OR(A=5)))+(35*((A>5)AND(A<10)))+
       (20*((A>=10)AND(A<15)))
```

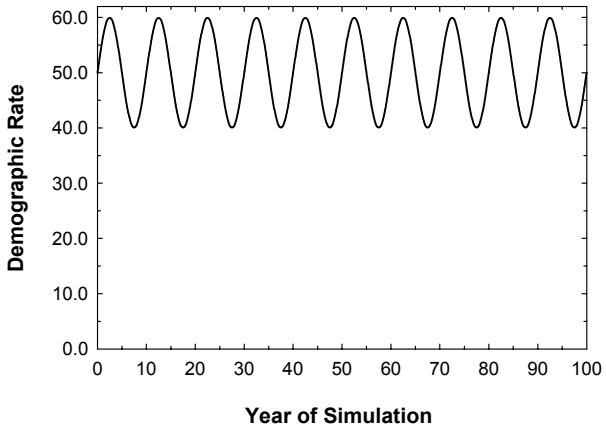
The rate increases stepwise with age, then drops to a lower level for years 10 through 14, and then drops to zero for animals 15 years and older. Note that although it can be tedious, any rate function can be modeled by specifying the rate for each interval of the dependent variable.



12. Cyclical response

```
RATE = 50+(10*SIN((PI*Y)/5))
```

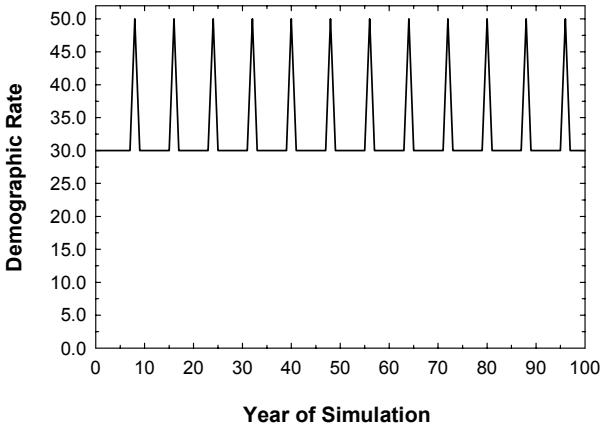
Here the rate fluctuates between 40 and 60 according to a sine wave with a 10-year periodicity.



13. Regular pulses of a higher rate

```
RATE = Y%8=0*20+30
```

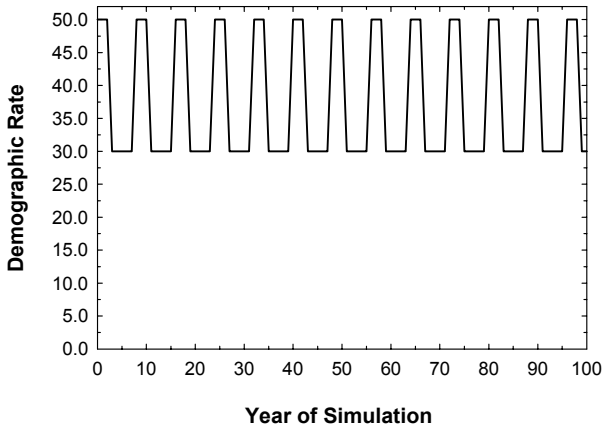
Background rate of 30 jumps to 50 every 8th year. Note that the order of operators was left to the *VORTEX* default (left to right). This is not a safe practice, but it does work in this case.



14. Pulses of longer duration

```
RATE = (((Y%8)<3)*20)+30
```

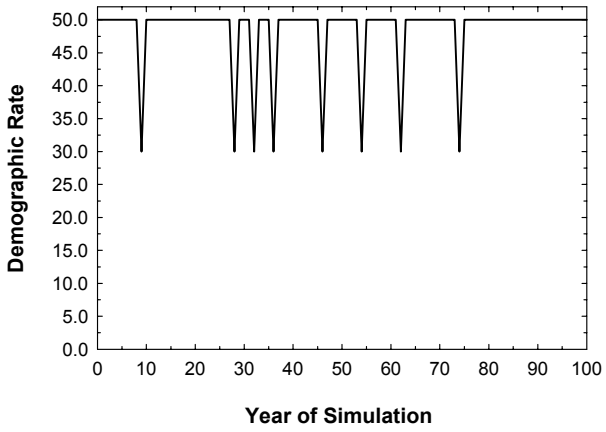
The rate jumps to 50 for a 3-year time span every 8th year. In this case, parentheses were used (wisely) to be sure that the intended order of operators was followed.



15. Random pulses: catastrophes

```
RATE = 50-(20*(SRAND(Y+(R*100))<0.05))
```

The background rate of 50 drops to 30 on average once every 20 years. A seeded random number is needed; otherwise the years in which the rate drops would be independent among individuals (effectively, the rate would continuously be 49). The seed of `Y+(R*100)` causes a different seed to be used for each year of each iteration (if there are 100 or fewer years). The above function is equivalent to specifying a catastrophe with frequency = 5% and severity = 0.60.



16. Random pulses independent among populations

```
RATE = 50-(20*[(SRAND[Y+(R*100)+(100*SRAND(P))])<0.05])
```

The "catastrophes" are independent among populations, because each population (**P**) sets a new (and random) seed for the random number generator which tests whether the catastrophe occurs. Careful use of parentheses (or brackets) is critical in this function, in order to ensure that the random number seeds work as intended.

17. Catastrophes affecting only selected age class(es)

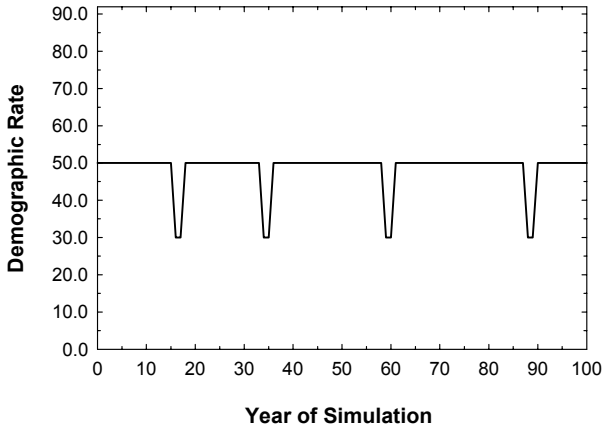
```
RATE = 50-((A<3)*20*(SRAND(Y+(R*100))<0.05))
```

The catastrophe affects only individuals of ages 1 and 2. The 2-D graphs of this function do not illustrate the age-dependent relationship: The graphs against **Y** and **R** set **A** = 1 (and show the catastrophes affecting young individuals); while the graph against **A** happens to display a year and iteration (**Y** = **R** =1) in which no catastrophe for any age occurs.

18. Multi-year catastrophes

```
RATE = 50-(20*(SRAND((Y/2)+(R*100))<0.10))
```

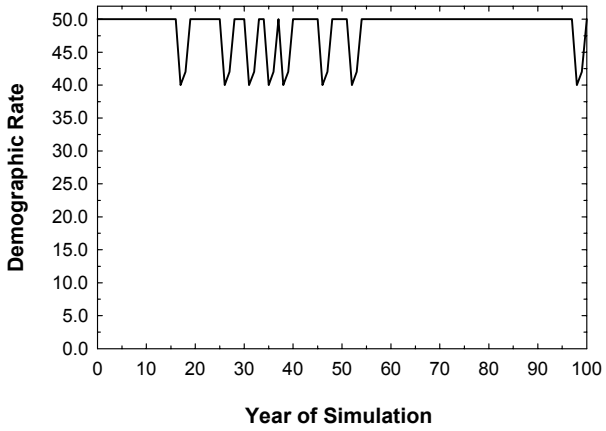
The catastrophes have a 2-year impact, because the seed value is converted to an integer, giving pairs of subsequent years the same random number. The frequency per year is 10%, so that the frequency of an onset of a 2-year catastrophe is 5%.



19. Multi-year catastrophes with a decreased impact in year 2

```
RATE = 50-([10*(SRAND(Y+(R*100))<0.05)]+[8*(SRAND((Y-1)+(R*100))<0.05)])
```

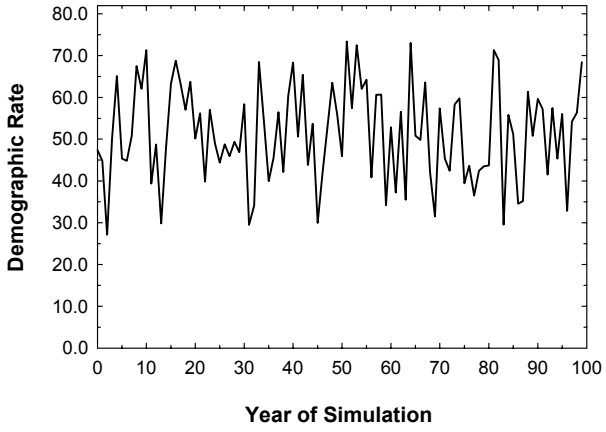
The second seed is the same as the first seed from the previous year. Thus the catastrophe has a lesser impact (severity = 0.84 rather than 0.80) in the second year. This approach can also be used to model catastrophes which impact survival in one year (using a function with an expression like that in the first brackets above) and fecundity in the second year (using a function containing the expression in the second set of brackets). Note that in example #18, catastrophes always start in even-numbered years, while in this example catastrophes can begin in any year.



20. Random variation across years

```
RATE = 50+[10*(SNRAND(Y+(R*100)))]
```

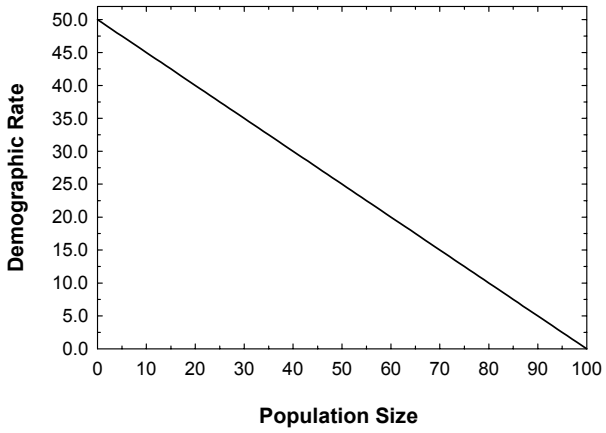
This is the same as imposing a mean rate of 50 with environmental variation of SD = 10.



21. Linear density dependence

```
RATE = 50*((K-N)/K)
```

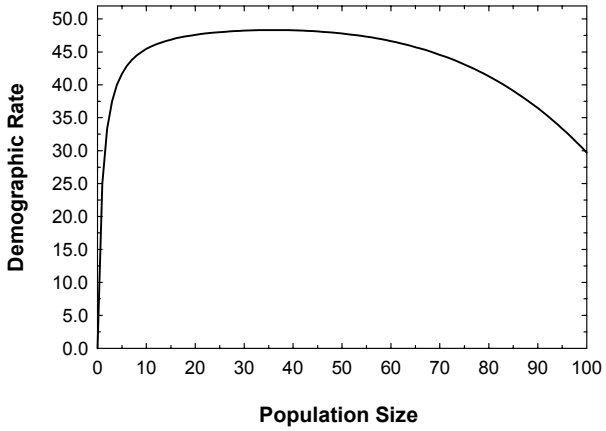
The rate declines from 50, at **N** = 0, to 0 when **N** = **K**.



22. Density dependence used as the default for breeding in *VORTEX*

```
RATE = [50-(20*[(N/K)^4])]*[N/(1+N)]
```

The rate peaks near 50 when N is small, declines at higher densities, and is 30 when **N** = **K**. At very small **N**, the rate is also depressed. For example, it is reduced by 50% when **N** = 1, and reduced by 25% when **N** = 3. In terms of the coefficients that can be entered into the optional density-dependence for breeding in *VORTEX*, **P(0)** = 50, **P(K)** = 30, **B** = 4, and **A** = 1.



23. Sex-specific dispersal rates

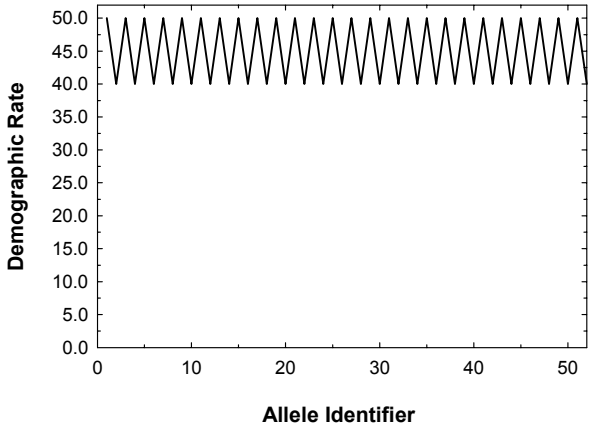
```
RATE = D*[(S='M')OR(RAND>0.35)]
```

If the above function is used for the Dispersal Modifier Function, then 35% of the females are prevented from dispersing. Thus, dispersal rates for females are effectively reduced by 35% relative to male dispersal. An unseeded random number is used so that dispersal will be determined independently each female. Note that the dispersal rates entered subsequently (**D**) will be those applied to males, with females having lower rates. A similar approach can be used to create age--specific dispersal rates (or dispersal mortality).

24. Alleles confer differential reproductive rates

```
RATE = 40+(10*(V%2))+(10*(Z%2))
```

In this case, half of the alleles (specifically, those with even numbers) cause an increment of 10 in the breeding rate of their carriers. An individual that is homozygous for an even-numbered allele will have a breeding rate equal to 60%, while those homozygous for an odd-numbered allele will have a rate equal to 40%.



25. Overdominance for survival, all unique founder alleles

```
RATE = 20+(10*(V=Z))
```

An infinite alleles model in which homozygotes have a mortality of 30%, while the rate for heterozygotes is 20%.

26. Overdominance for survival, two functionally distinct founder alleles

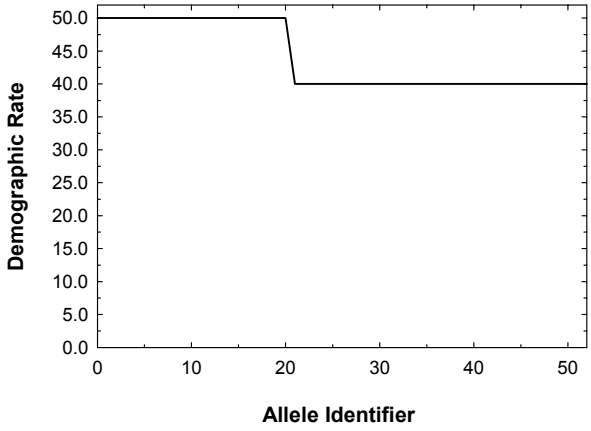
```
RATE = 20+(10*((V%2)=(Z%2)))
```

A two allele model in which homozygotes with two odd or two even alleles have a mortality of 30%, while the rate for heterozygotes is 20%.

27. Outbreeding depression for breeding rate upon introgression from supplemented individuals

```
RATE = 50-(10*((V<20)=(Z>19)))
```

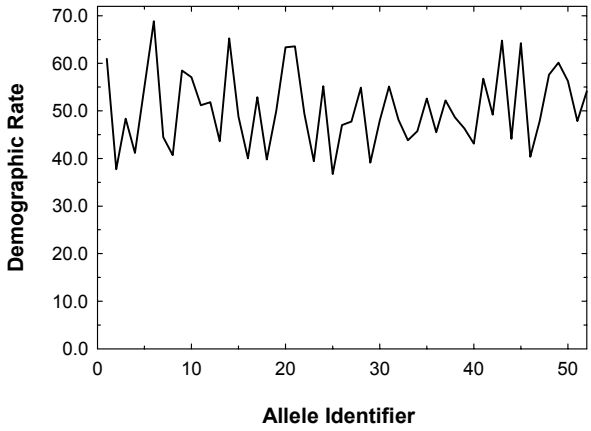
With ten initial founders, and with some number of individuals from another source used as supplements at a later stage, the breeding rate is 50% for an individual which carries both of its alleles from the initial founders, or both from the source population of the supplements, vs. 40 for individuals which are heterozygous, carrying an allele from each source.



28. Genetically-based individual variation in breeding success

```
RATE = 50+(5*(SNRAND((R*100)+V)+SNRAND((R*100)+Z)))
```

In this case, breeding rates vary around a mean of 50 with a standard deviation equal to 5*SQRT(2).



29. Density dependence, relative to the average density across populations 1 and 2

```
RATE = 50*([KK(1)+KK(2)]-[NN(1)+NN(2)])/[KK(1)+KK(2)])
```

Note the use of `KK(p)` and `NN(p)` to indicate `K` and `N` for population `p`.

Appendix

I

An Overview of Population Viability Analysis Using *VORTEX*

Introduction

This Appendix presents an overview of processes threatening the health and persistence of wildlife populations, the methods of population viability analysis, the *VORTEX* simulation program for PVA, and the application of such techniques to wildlife conservation. Much of the following material is adapted from Lacy (1993a) and Lacy (1993/4).

The Dynamics of Small Populations

Many wildlife populations that were once widespread, numerous, and occupying contiguous habitat have been reduced to one or more small, isolated populations. The primary causes of the decline of many species are obvious and deterministic: Populations are over-harvested; natural habitat is converted and lost to the species, often involving the replacement of diverse ecological communities with monocultures; environments are polluted, with the dumping of toxins into the air, water, and soil; local and now even global climates are modified by the actions of humans; and numerous exotic competitors, predators, parasites and diseases are introduced into communities that have never evolved defenses to the new invaders. The primary causes of species decline are usually easy to understand, and often easy to study and model, but usually, though not always, difficult to reverse. Even if the original causes of decline are removed, a small isolated population is vulnerable to additional forces, intrinsic to the dynamics of small populations, which may drive the population to extinction (Shaffer 1981; Soulé 1987; Clark and Seebeck 1990).

Of particular impact on small populations are stochastic, or random or probabilistic, processes. Indeed, the final extinction of most populations often occurs not so much because of a continuation of the pressures that led to the initial decline, but because of bad luck. Chance, or stochastic, processes usually have little impact on long-term population dynamics, as long as the population is abundant and spread over a wide geographic range and a number of habitats. Deterministic processes, such as those listed above, predominate in widespread, still common species, while local chance events impacting subsets of the population will average out across the broader, diverse range. When a population becomes small, isolated, and localized, however, chance events can become important, even dominating the long-term dynamics and fate of a population.

Many stages in the life history of an organism, and the processes that define the history of a biological population, are essentially stochastic sampling phenomena. Births, deaths, dispersal, disease, sex determination, and transmission of genes between generations all are largely probabilistic phenomena. Small samples intrinsically have greater variance around the probabilistic mean or expectation than do large samples, and therefore small populations will experience greater fluctuations in births, deaths, sex ratio, and genetic variation than will larger populations. The fundamental problem facing small populations is that the fluctuations they experience due to the multiple stages of sampling each generation make it increasingly likely that the populations will, unpredictably, decline to zero. Once populations are small, the probability that they will become extinct can become more strongly determined by the amount of fluctuations in population size than in the mean, deterministic population growth rate. Thus, extinction can be viewed as a process in which once common and widespread populations become reduced to small, isolated fragments due to extrinsic factors, the small remnant populations then become subjected to large fluctuations due to intrinsic processes, the local populations occasionally and unpredictably go extinct, and the cumulative result of local extinctions is the eventual extinction of the taxon over much or all of its original range (Gilpin and Soulé 1986; Clark et al. 1990).

The stochastic processes impacting on populations have been usefully categorized into demographic stochasticity, environmental variation, catastrophic events, and genetic drift (Shaffer 1981). Demographic stochasticity is the random fluctuation in the observed birth rate, death rate, and sex ratio of a population even if the probabilities of birth and death remain constant. Assuming that births and deaths and sex determination are stochastic sampling processes, the annual variations in numbers that are born, die, and are of each sex can be specified from statistical theory and would follow binomial distributions. Such demographic stochasticity will be most important to population viability perhaps only in populations that are smaller than a few tens of animals (Goodman 1987), in which cases the annual frequencies of birth and death events and the sex ratios can deviate far from the means.

Environmental variation is the fluctuation in the probabilities of birth and death that results from fluctuations in the environment. Weather, the prevalence of enzootic disease, the abundances of prey and predators, and the availability of nest sites or other required microhabitats can all vary, randomly or cyclically, over time. The fluctuations in demographic rates caused by environmental variation is additive to the random fluctuations due to demographic stochasticity. Thus, the difference between the observed variation in a demographic rate over time and the distribution describing demographic variation must be accounted for by environmental variation.

Catastrophic variation is the extreme of environmental variation, but for both methodological and conceptual reasons rare catastrophic events are analyzed separately from the more typical annual or seasonal fluctuations. Catastrophes such as epidemic disease, hurricanes, large-scale fires, and floods are outliers in the distributions of environmental variation. As a result, they have quantitatively and sometimes qualitatively different impacts on wildlife populations. (A forest fire is not just a very hot day.) Such events often precipitate the final decline to extinction (Simberloff 1986, 1988). For example, one of two populations of whooping crane was decimated by a hurricane in 1940 and soon after went extinct (Doughty 1989). The only remaining population of the black-footed ferret (*Mustela nigripes*) was being eliminated by an outbreak of distemper when the last 18 ferrets were captured (Clark 1989).

Genetic drift is the cumulative and non-adaptive fluctuation in allele frequencies resulting from the random sampling of genes in each generation. This can impede the recovery or accelerate the decline of wildlife populations for several reasons (Lacy 1993b). Inbreeding, not strictly a component of genetic drift but correlated with it in small populations, has been documented to cause loss of fitness in a wide variety of species, including virtually all sexually reproducing animals in which the effects of inbreeding have been carefully studied (Wright 1977; Falconer 1981; O'Brien and Evermann 1988; Ralls et al. 1988; Lacy et al. 1993; Lacy 1997). Even if the immediate loss of fitness of inbred individuals is not large, the

loss of genetic variation that results from genetic drift may reduce the ability of a population to adapt to future changes in the environment (Fisher 1958; Robertson 1960; Selander 1983).

Thus, the effects of genetic drift and consequent loss of genetic variation in individuals and populations negatively impact on demographic rates and increase susceptibility to environmental perturbations and catastrophes. Reduced population growth and greater fluctuations in numbers in turn accelerates genetic drift (Crow and Kimura 1970). These synergistic destabilizing effects of stochastic process on small populations of wildlife have been described as "extinction vortices" (Gilpin and Soulé 1986).

What is Population (and Habitat) Viability Analysis?

Analyses which have used the *VORTEX* simulation for guiding conservation decisions refer variously to "Population Viability Analysis (PVA)", "Population and Habitat Viability Analysis (PHVA)," "Population Vulnerability Analysis", "Population Viability (or Vulnerability) Assessment", and other variants on the name. This diversity of terminology has caused some confusion among practitioners of the PVA (or PHVA) approach, and probably even more confusion among wildlife managers who have tried to understand what analysis was being described, and whether it could be a useful tool in their efforts to conserve biodiversity. The diversity of perceptions about the PVA approach is not limited to its name. Different people mean different things by PVA, and the definitions and practice of PVA are constantly evolving. We don't think it is not the case, as has sometimes been suggested, that some people are doing PVA correctly, and others incorrectly, but rather that people are using different (if related) kinds of analyses and labeling them with the same (or similar) terms. What analysis is correct depends on the need and the application. Below, we attempt to clarify what PVA is, by suggesting a more consistent terminology and by describing the features that characterize the application of the PVA approach to conservation. The perspective offered here is necessarily biased by personal experiences in conservation; we will not attempt an exhaustive historical account of this field.

Population viability analysis originally described methods of quantitative analysis to determine the probability of extinction of a population. Shaffer (1981) first defined a minimum viable population (MVP) as the size at which a population has a 99% probability of persistence for 1000 years, but it might be more meaningful biologically to consider it to be the size below which a population's fate becomes determined largely by the stochastic factors that characterize extinction vortices. One concept of population viability analysis is any methodology used to determine an MVP (Shaffer 1990). More broadly, PVA is the estimation of extinction probabilities and other measures of population performance by analyses that incorporate identifiable threats to population survival into models of the extinction process (Brussard 1985; Gilpin and Soulé 1986; Burgman et al. 1993; Lacy 1993/1994).

Shaffer's (1981) original term "minimum viable population" (MVP) has fallen into disfavor (Soulé 1987), even as the PVA approach has risen in popularity. Shaffer stressed that an MVP was an estimate of the population size below which the *probability* of extinction was unacceptably high, that different populations would have different MVPs, and that the MVP determined for a population would depend on the threatening factors that were considered. However, the term implied to some people that there was a well-defined number below which extinction was certain and above which persistence was assured. Re-emphasizing the probabilistic nature of the extinction process, a number of conservation biologists have focused on methods for estimating the probability of extinction over defined time periods for a designated population exposed to a specific scenario of environmental conditions, threats to persistence, and future management actions and other foreseeable events (Brussard 1985; Starfield and Bleloch 1986; Soulé 1987; Simberloff 1988; Gilpin 1989; Shaffer 1990; Boyce 1992; Burgman et al. 1993). Thus, "Population Viability Analysis" (or the synonymous "Population Viability Assessment" and "Population Vulnerability Analysis") came to describe any of the array of methods for quantifying the probability of extinction of a

population. Although PVA has been extended by some to encompass a broader approach to conservation (see below), the term "Population Viability Analysis", or PVA, should perhaps be reserved for its original, yet still rather broad, meaning.

Beginning in about 1989 (Lacy et al. 1989; Seal and Lacy 1989; Seal et al. 1990), it became increasingly recognized that PVA can often be most usefully incorporated into a strategy for the conservation of a taxon if it is part of, and often central to, a conservation workshop that mobilizes collaboration among the array of people with strong interest in or responsibility for a conservation effort (e.g., governmental wildlife agencies, conservation NGOs, and the local people who interact with the species or its habitat) or with particular expert knowledge about the species, its habitats, or the threats it faces (e.g., academic biologists, conservation professionals, other wildlife biologists, experts on human demographics and resource use). Conservation problems are almost always multi-faceted, involving not only complex dynamics of biological populations, but also interactions with human populations, the past, present, and future impacts of humans on habitats, and human political, social, and economic systems (Alvarez 1993; Bormann and Kellert 1991; Clark 1989, 1993). Many people need to contribute knowledge, expertise, and ideas in order to achieve the recovery of threatened species. Population viability analyses can provide a framework for incorporating the many needed kinds of knowledge into species conservation efforts, because PVAs do allow the assessment of many kinds of factors that threaten the persistence of populations (Lacy 1993a; Lindenmayer et al. 1993).

The Conservation Breeding Specialist Group (CBSG) of the IUCN's Species Survival Commission especially has advocated and used workshops centered on PVAs to provide guidance to conservation assessment and planning (see references to CBSG workshops in Appendix III). Over the past few years, the PVA workshop as an approach to species conservation has expanded considerably beyond the quantitative analysis of extinction probabilities as advanced by Shaffer (1981, 1990), Soulé (1987), Gilpin (1989), Clark et al. (1991), Boyce (1992), and others. PVA workshops have incorporated consideration of resource use and needs by local human populations (Seal et al. 1991; Bonaccorso et al. 1999), education programs for the local human populations (Odum et al. 1993), trade issues (Foose et al. 1993), and trends in human demographics and land use patterns (Walker and Molur 1994; Herrero and Seal 2000). Recognizing that the conservation assessment workshops increasingly incorporated more than just the population biology modeling (which still formed a core organizing and analysis framework for the workshop), the CBSG has termed their workshops Population *and Habitat* Viability Analyses (PHVA). We would recommend that the term Population and Habitat Viability Analysis (PHVA) be used to describe the collaborative workshop approach to species conservation that centers on, but encompasses more than, a Population Viability Analysis (in the narrow sense). The concept of a PHVA continues to expand and evolve, as it should considering the need for more holistic and flexible approaches to conservation (e.g., Ruggiero et al. 1994). Thus, in the usage I recommend, PVA is a quantitative analysis of the probability of population persistence under defined sets of assumptions and circumstances. PHVA is a workshop process that brings to bear the knowledge of many people on species conservation, eliciting and assessing multiple options for conservation action, principally by using the tool of PVA as a way evaluate present threats to population persistence and likely fates under various possible scenarios.

Population Viability Analysis (PVA)

Two defining characteristics of a PVA are an explicit model of the extinction process and the quantification of threats to extinction. These features set PVA apart from many other analyses of the threats facing species, including, for example, the IUCN Red Books of Threatened Species. As a methodology to estimate the probability of extinction of a taxon, PVA necessarily must start with an understanding, or model, of the extinction process (Clark et al. 1990).

Generally, the model of extinction underlying a PVA considers two categories of factors: deterministic and stochastic. Deterministic factors, those that can shift species from long-term average population growth to population decline include the well-known threats of over-harvest, habitat destruction, pollution or other degradation of environmental quality, and the introduction of exotic predators, competitors, and diseases. Singly or combined, these forces have driven many wildlife populations to low numbers and, for some, to extinction. Once a population becomes small, and isolated from conspecific populations that might serve as sources for immigrants that could stabilize demographics and genetics, its dynamics and fate can become dominated by a number of random or stochastic processes (as outlined above and by Shaffer 1981). Thus, even if the original deterministic causes of decline are stopped or reversed, the instability caused by the action of stochastic processes acting on small populations can cause the extinction of a population.

In nature, most threatening processes have both deterministic and stochastic features. For example, a high level of poaching might be seen as a deterministic factor driving a wildlife population toward extinction, but whether an individual animal is killed might be largely a matter of chance. In a PVA, poaching might be modeled as a deterministic process by killing a determined proportion of the animals, or it might be modeled as a stochastic process by giving each animal that probability of being killed but allowing the exact numbers killed to vary over time. If the population is large and the percent of animals killed is high, then these two ways of modelling the effects of poaching will yield the same results: the deterministic component of poaching dominates the population dynamics. If the population is small or the percent of animals killed is very low, then the numbers killed in a stochastic model (and in nature) might vary substantially from year to year: the stochastic nature of poaching further destabilizes the population.

Which of the various deterministic and stochastic factors are important to consider in a PVA will depend on the species biology, the present population size and distribution, and the threats it faces. For example, orang utans may be threatened by forest destruction and other largely deterministic processes, but inbreeding and randomly skewed sex ratios resulting from highly stochastic processes are unlikely to be problems, at least not on a species-wide basis. On the other hand, even if the remnant Atlantic coastal rainforest of Brazil is secured for the future, the populations of golden lion tamarins (*Leontopithecus rosalia*) which can persist in that remnant forest are not sufficiently large to be stable in the face of stochastic threats (Seal et al. 1990; Rylands 1993/4; Ballou et al. 1997). The identification of the primary threats facing a taxon via a comprehensive PVA is important for conservation planning. For example, tamarin populations might be stabilized by the translocations and reintroductions that are underway and planned, but an orang utan PHVA recognized that releases of confiscated "pet" orang utans are unlikely to have a conservation benefit for those populations which are facing habitat destruction, not stochastic fluctuations and inbreeding. For many species, such as the whooping crane (*Grus americana*), the temporarily extinct-in-the-wild black-footed ferret (*Mustela nigripes*), and the Puerto Rican parrot (*Amazona vitatta*), only a single population persisted in the wild. Although those populations may have been maintained or even increased for a number of years, the principal threat was that a local catastrophe (e.g., disease epidemic, severe storm) could decimate the population (Clark 1989; Lacy et al. 1989; Mirande et al. 1991). The primary recovery actions therefore needed to include the establishment of additional populations. Tragically, some taxa, such the eastern barred bandicoot (*Perameles gunnii*) in Australia, may be critically threatened simultaneously by deterministic factors and stochastic processes (Lacy and Clark 1990).

PVA is formally an assessment of the probability of extinction, but PVA methods often focus on other indicators of population health. Mean and variance in population growth (Lindenmayer and Lacy 1995a, 1995b, 1995c), changes in range, distribution, and habitat occupancy (Hanski and Gilpin 1991, 1997), and losses of genetic variability (Soulé et al. 1986; Lande and Barrowclough 1987; Seal 1992; Lacy and Lindenmayer 1995) can be analyzed and monitored. Although not yet common, monitoring of population health could also utilize measures of developmental stability (Clarke 1995), physiological parameters

such as body condition (Altmann et al. 1993) or levels of the hormones related to stress and reproduction (Sapolsky 1982, 1986), or the stability of behavior and the social structure of the population (Samuels and Altmann 1991).

The interactions and synergism among threatening processes will often cause numerical, distributional, physiologic, behavioral, and genetic responses to concordantly reflect species decline and vulnerability. It remains important, however, to understand and target the primary causal factors in species vulnerability. The recent proposal to base IUCN categories of threat on quantified criteria of probability of extinction, or changes in such indicators as species range, numbers, and trends (Mace and Lande 1991; Mace et al. 1992; Mace and Stuart 1994; IUCN Species Survival Commission 1994) reflects the increased understanding of the extinction process that has accompanied the development of PVA, and simultaneously demands that much more progress be made in developing predictive models, gathering relevant data on status and threats, and applying the PVA techniques.

Population and Habitat Viability Analysis (PHVA)

Population and Habitat Viability Analysis is a multi-faceted process or framework for assisting conservation planning, rather than a singular technique or tool. It is often interwoven with other techniques for managing complex systems, such as decision analysis (Maguire 1986; Maguire et al. 1990). Even when viewed as *the* PHVA workshop, all such conservation workshops involved and required substantial pre-workshop and post-workshop activities. Some PHVA workshops have been extended into multiple workshops and less formal, smaller collaborative meetings, often focused on subsets of the larger problems of species conservation.

Although PHVAs are diverse and not well defined, the PHVA process contains a number of critical components. First, it is essential to gather an array of experts who have knowledge of the species or problem. A PHVA is not required to bring together experts, but it often facilitates such sharing of expertise because the collective knowledge of many is essential for a useful PVA (in the narrow sense) to be completed. In addition to a diversity of people, a PHVA workshop also requires and therefore facilitates the involvement of a number of agencies and other concerned organizations. For example, the PVA on the two endemic primates of the Tana River Primate Reserve in Kenya (Seal et al. 1991) was convened by the Kenya Wildlife Service, facilitated by the IUCN SSC Captive Breeding Specialist Group, benefited from the expertise contributed by members of the IUCN SSC Primate Specialist Group, and was sponsored by the World Bank. The involvement of many agencies and interested parties is critical to endangered species recovery.

An early requirement, or prerequisite, of a PHVA workshop is to determine the conservation problem to be addressed, and to state the goals of the management plan. Many endangered species programs have not clearly identified their goals. For example, at a PHVA and Conservation Assessment and Management Plan workshop on the forest birds of the Hawaiian islands (Ellis et al. 1992a, 1992b), it became apparent that the agencies responsible for the conservation of Hawaii's bird fauna had not determined whether their goal was to prevent species extinctions, prevent taxa (species or subspecies) from becoming extirpated on any of the islands they presently inhabit, preserve species in sufficient numbers and distribution to allow them to continue to fill ecological roles in the biological communities, or the restoration of taxa to most or all parts of the original ranges. The management actions required to achieve these various levels of conservation are quite different. In contrast, a PHVA on the Grizzly Bear in the Central Rockies of Canada (Herrero and Seal 2000) clearly identified that provincial policy called for maintenance of stable or growing populations of the species. Thus, the criterion against which alternative management scenarios were judged was whether the PVA projections indicated that the populations would not decline.

PHVA workshops facilitate the assembly of all available data. Often, important information is found in the field notes of researchers or managers, in the heads of those who have worked with and thought about the problems of the species, and in unpublished agency reports, as well as in the published scientific literature. A pending PHVA can be the impetus that encourages the collection of data in anticipation of presentation, review, and analysis at the workshop. For example, a Sumatran Tiger PHVA helped stimulate the systematic collection of data on sightings and signs of tigers in protected areas throughout the island of Sumatra, and collation and integration with a Geographic Information System (GIS) map of habitats and human pressures on those habitats. The PHVA on the Grizzly Bear in the Central Canadian Rockies Ecosystem provided the opportunity for detailed habitat mapping data to be integrated with population biology data on the bears, resulting in the development of models which would allow projection of the impacts of habitat changes on the bear populations.

It is important to specify the assumptions that underlay a PHVA, and any consequent management recommendation. For example, the Hawaiian bird conservation efforts are constrained by a belief that no birds bred outside of the islands should ever be brought back to the islands for release. While this position derives from a reasonable concern for disease transmission (much of the decline of Hawaii's native birds is thought to be due to introduced avian diseases) as much as from any political or philosophical stand, any justification for the restriction must be questioned in light of the fact that wildlife agencies import and release, without quarantine, 1000s of exotic gamebirds onto the islands annually.

Once experts are assembled, problems stated and goals set, data gathered, and assumptions specified, then the PHVA process can proceed with what I describe as PVA in the narrow sense: estimation of the probability of population persistence. The available data are used to estimate the parameters that are needed for the model of population dynamics to be applied. Often, data are not available from which to estimate certain key parameters. In those cases, subjective and objective, but non-quantified, information might be solicited from the assembled experts, values might be obtained from data on related species, or a factor might simply be omitted from the model. While such a non-precise process might consist simply of intuitive judgements made by experts, it is important to specify how values for the parameters in the model were obtained. The resulting limitations of the analyses should be acknowledged, and a decision made if, how, by whom, and when the missing data would be collected so that more refined analyses could be conducted. With the PVA model, projections of the most likely fate, and distribution of possible fates, of the population under the specified assumptions are made.

Because so much of a PVA – the data, the model, and even the interpretation of output – is uncertain, a PVA that provides an estimate of the probability of extinction under a single scenario is of very limited usefulness. An essential component of the PHVA process, therefore, is sensitivity testing. Ranges of plausible values for uncertain parameters should be tested, to determine what effects those uncertainties might have on the results. In addition, several different PVA models might be examined at a PHVA workshop, or the same general model tested under different structural assumptions. Different participants in the process should assess and interpret the results. Such sensitivity testing reveals which components of the data, model, and interpretation have the largest impact on the population projections. This will indicate which aspects of the biology of the population and its situation contribute most to its vulnerability and, therefore, which aspects might be most effectively targeted for management. In addition, uncertain parameters that have a strong impact on results are those which might be the focus of future research efforts, to better specify the dynamics of the population. Close monitoring of such parameters might also be important for testing the assumptions behind the selected management options and for assessing the success of conservation efforts.

Closely parallel to the testing of uncertainties in the present situation is the testing of options for management. PVA modeling allows one to test the expected results of any given management action, under the assumptions of the model and within the limitations of present knowledge, on the computer

before implementation in the field. This process can guide selection of the management options most likely, given current knowledge, to be effective, and will define target recovery goals that should be obtained if our knowledge is adequate and the recommended actions are followed. A PHVA workshop on the Black Rhinoceros in Kenya's 11 rhino sanctuaries (Foose et al. 1993) suggested that periodic movement of rhinos between fenced sanctuaries to reduce inbreeding and demographic fluctuations would be necessary to stabilize the populations in the smaller parks. Moreover, the modeling provided estimates of the rate at which the larger populations would be able to provide surplus animals for translocation.

It would be an error to assume that any PVA model incorporates everything of interest. A PVA simulation program can only include those processes that are known to the programmer. This will likely be a subset of what might be known to the field biologists, which in turn will definitely be a subset of those processes that impact natural populations. A number of variables affecting population dynamics and viability are not yet commonly examined in PVA models. These include: social and ecological determinants of dispersal; complex social processes, such as the role of non-breeders in group stability and the impacts of other aspects of the social environment on reproductive success and survival; competitive, exploitative, or mutualistic interactions with other species experiencing their own population dynamics; and the effects of changes in the global environment. To date, most PVA models treat organisms as independent actors in spatially homogeneous physical, biotic, and social environments. There is tremendous opportunity and need for elaboration of PVA models, and it is likely that increasingly sophisticated models will also become more specific to the individual taxa and environments under study.

PHVA workshops must incorporate consideration of the assumptions of the PVA model used and the biases or limitations in interpretation that could result. PHVAs consider only those threatening processes of which we have knowledge, for which we can develop algorithms for modeling or other methods for analysis, and for which we have some data. As a result, it is likely that PVAs will underestimate the vulnerability of most populations to extinction, and that PHVA workshops will be less comprehensive than is desirable. We need always to be cognizant of the limits of our understanding of wildlife populations, and to include appropriate margins for error in our conservation strategies.

PVA is, by definition, an assessment of the probability of persistence of a population over a defined time frame. Yet, persistence of a population, while a necessary condition for effective conservation of natural systems, is often not sufficient. Prevention of extinction is the last stand of conservationists, but the goals should be higher: conservation of functional biological communities and ecosystems. PVA usually ignores the functional role of a species in a community, but a PHVA workshop should consider much more than the prevention of the final biological extinction of the taxon. A species, such as the American Bison (*Bison bison*), can be functionally extinct in terms of no longer filling its original role in nature, even as it is praised as a conservation success story and would be considered safe from extinction and viable.

The use of the PHVA process to help guide conservation decisions is not a singular event, in which an analysis can be completed, management actions recommended and implemented, and conservation thereby assured. The many uncertainties in the process mandate that PVA be used as a tool in an adaptive management framework, and a PHVA workshop is just one stage of an effective conservation strategy. In adaptive management, the lack of knowledge adequate to predict with certainty the best course of action is recognized, management actions are designed in such a way that monitoring will allow testing of the adequacy of our model and understanding, and corrective adjustments to management plans are made whenever the accumulating data suggest that the present course is inadequate to achieve the goals and that a better strategy exists (Holling 1978). The urgency of the biodiversity crisis will not permit us ethically to refrain from aggressive conservation action until we have scientifically sound understanding of all the

factors that drive population, community, and ecosystem dynamics. PHVA provides a forum for making use of the information we do have, in a well-documented process that is open to challenge and improvement. PHVA workshops can, therefore, assist wildlife managers in the very difficult and important job of using science to safeguard the future of wildlife populations.

In summary, Population Viability Analysis (PVA) and Population and Habitat Viability Analysis (PHVA) refer to an array of interrelated and evolving techniques for assessing the survival probability of a population and possible conservation actions. It might be useful to restrict the term PVA to its original meaning -- the use of quantitative techniques to estimate the probability of population persistence under a chosen model of population dynamics, a specified set of biological and environmental parameters, and enumerated assumptions about human activities and impacts on the system. PHVA refers to a workshop approach to conservation planning, which elicits and encourages contributions from an array of experts and stakeholders, uses PVA and other quantitative and non-quantitative techniques to assess possible conservation actions, and strives to achieve consensus on the best course of action from competing interests and perspectives, incomplete knowledge, and an uncertain future.

Many of the components of PVAs and PHVAs, even when used in isolation, can be effective educational and research tools. To be a useful framework for advancing the conservation of biodiversity, however, PHVA must incorporate all of: (1) collection of data on the biology of the taxon, status of its habitat, and threats to its persistence, (2) quantitative analysis of available data, (3) input of population status and identifiable threats to persistence into analytical or simulation models of the extinction process, (4) assessment of the probability of survival over specified periods of time, given the assumptions and limitations of the data and model used, (5) sensitivity testing of estimates of extinction probability across the range of plausible values of uncertain parameters, (6) specification of conservation goals for the population, (7) identification of options for management, (8) projection of the probability of population survival under alternative scenarios for future conservation action, (9) implementation of optimal actions for assuring accomplishment of conservation goals, (10) continued monitoring of the population, (11) reassessment of assumptions, data, models, and options, and (12) adjustment of conservation strategies to respond to the best information available at all times. There are many uncertain aspects of population dynamics, especially of endangered taxa, including few data on species biology and habitats, uncertain political and social climate for implementing conservation actions, and the unpredictability inherent in small populations due to the many stochastic forces that drive population dynamics.

The rapid development of PVA as a research and management tool, and the concurrent but not always parallel expansion of the scope of what conservation threats, options, and actions are considered in PHVA workshops, has led to confusion. Different people can describe rather distinct kinds of analyses with the same terminology, while others use different terms to describe nearly identical approaches. The ever-changing concepts of PVA and PHVA are confusing, but the flexibility of the processes is also their strength. Current tools are inadequate to address fully the challenges of stemming the losses of biodiversity. The PVA/PHVA framework allows and encourages rapid application of new tools, data, and interpretations into increasingly effective conservation programs.

Methods for Analyzing Population Viability

An understanding of the multiple, interacting forces that contribute to extinction vortices is a prerequisite for the study of extinction-recolonization dynamics in natural populations inhabiting patchy environments (Gilpin 1987), the management of small populations (Clark and Seebeck 1990), and the conservation of threatened wildlife (Shaffer 1981, 1990; Soulé 1987; Mace and Lande 1991).

Shaffer (1981) suggested several ways to conduct PVAs. Perhaps the most rigorous method, and the one that would produce the most defensible estimates, would be an empirical observation of the stability and long term fates of a number of populations of various sizes. Berger (1990) presented a good example of this approach, in which he observed that populations of bighorn sheep in the mountains of the western USA persisted only when the populations consisted of more than 100 animals. A few other studies of wildlife populations have provided empirical data on the relationship between population size and probability of extinction (e.g., Belovsky 1987; Thomas 1990), but presently only order of magnitude estimates can be provided for MVPs of vertebrates (Shaffer 1987). More empirical studies are needed, but the time and numbers of populations required for such studies are precluded in the cases of most species threatened with extinction -- exactly those for which estimates of population vulnerability are most urgently needed.

A more elegant and general approach to PVA is to develop analytical models of the extinction process that will allow calculation of the probability of extinction from a small number of measurable parameters. Goodman's (1987) model of demographic fluctuations, and applications to conservation of the classic population genetic models of loss of genetic diversity by genetic drift (Franklin 1980; Soulé et al. 1986; Lande and Barrowclough 1987) are valuable efforts in this direction. Unfortunately, our understanding of population biology is not yet sufficient to provide fully adequate analytical models of the extinction process. For example, none of the existing analytical models incorporate all three of demographic, environmental, and genetic fluctuations, and thus they do not begin to model the array of extinction vortices described by Gilpin and Soulé (1986). Moreover, the analytical models make extremely simplifying assumptions about a number of the intricacies of population structure. For example, social groupings or preferences are often assumed to be invariant or lacking, resulting in random mating; and dispersal is usually assumed to be random between all sites (the "island model") or only to occur between adjacent sites (the "stepping stone model"). Much more work is needed either to develop more complex and flexible models or to demonstrate that the simple models are sufficient to provide guidance for conservation.

A third method of conducting a PVA is the use of computer simulation modeling to project the probability distribution of possible fates of a population. Simulation models can incorporate a very large number of threatening processes and their interactions, if the processes can be described in terms of quantitative algorithms and parameterized. Although many processes affecting small populations are intrinsically indeterminate, the average long-term fate of a population and the variance around the expectation can be studied with computer simulation models. The focus is on detailed and explicit modeling of the forces impinging on a given population, place, and time of interest, rather than on delineation of rules (which may not exist) that apply generally to most wildlife populations.

Modeling and Population Viability Analysis

A model is any simplified representation of a real system. We use models in all aspects of our lives, in order to: (1) extract the important trends from complex processes, (2) permit comparison among systems, (3) facilitate analysis of causes of processes acting on the system, and (4) make predictions about the future. A complete description of a natural system, if it were possible, would often decrease our understanding relative to that provided by a good model, because there is "noise" in the system that is extraneous to the processes we wish to understand. For example, the typical representation of the growth of a wildlife population by an annual percent growth rate is a simplified mathematical model of the much more complex changes in population size. Representing population growth as an annual percent change assumes constant exponential growth, ignoring the irregular fluctuations as individuals are born or immigrate, and die or emigrate. For many purposes, such a simplified model of population growth is very useful, because it captures the essential information we might need regarding the average change in

population size, and it allows us to make predictions about the future size of the population. A detailed description of the exact changes in numbers of individuals, while a true description of the population, would often be of much less value because the essential pattern would be obscured, and it would be difficult or impossible to make predictions about the future population size.

In considerations of the vulnerability of a population to extinction, as is so often required for conservation planning and management, the simple model of population growth as a constant annual rate of change is inadequate for our needs. The fluctuations in population size that are omitted from the standard ecological models of population change can cause population extinction, and therefore are often the primary focus of concern. In order to understand and predict the vulnerability of a wildlife population to extinction, we need to use a model which incorporates the processes which cause fluctuations in the population, as well as those which control the long-term trends in population size. Many processes can cause fluctuations in population size: variation in the environment (such as weather, food supplies, and predation), genetic changes in the population (such as genetic drift, inbreeding, and response to natural selection), catastrophic effects (such as disease epidemics, floods, and droughts), decimation of the population or its habitats by humans, the chance results of the probabilistic events in the lives of individuals (sex determination, location of mates, breeding success, survival), and interactions among these factors (Gilpin and Soulé 1986).

Models of population dynamics which incorporate causes of fluctuations in population size in order to predict probabilities of extinction, and to help identify the processes which contribute to a population's vulnerability, are used in Population Viability Analysis (PVA). For the purpose of predicting vulnerability to extinction, any and all population processes that impact population dynamics can be important. Much analysis of conservation issues is conducted by largely intuitive assessments by biologists with experience with the system. Assessments by experts can be quite valuable, and are often contrasted with "models" used to evaluate population vulnerability to extinction. Such a contrast is not valid, however, as *any* synthesis of facts and understanding of processes constitutes a model, even if it is a mental model within the mind of the expert and perhaps only vaguely specified to others (or even to the expert himself or herself).

A number of properties of the problem of assessing vulnerability of a population to extinction make it difficult to rely on mental or intuitive models. Numerous processes impact population dynamics, and many of the factors interact in complex ways. For example, increased fragmentation of habitat can make it more difficult to locate mates, can lead to greater mortality as individuals disperse greater distances across unsuitable habitat, and can lead to increased inbreeding which in turn can further reduce ability to attract mates and to survive. In addition, many of the processes impacting population dynamics are intrinsically probabilistic, with a random component. Sex determination, disease, predation, mate acquisition -- indeed, almost all events in the life of an individual -- are stochastic events, occurring with certain probabilities rather than with absolute certainty at any given time. The consequences of factors influencing population dynamics are often delayed for years or even generations. With a long-lived species, a population might persist for 20 to 40 years beyond the emergence of factors that ultimately cause extinction. Humans can synthesize mentally only a few factors at a time, most people have difficulty assessing probabilities intuitively, and it is difficult to consider delayed effects. Moreover, the data needed for models of population dynamics are often very uncertain. Optimal decision-making when data are uncertain is difficult, as it involves correct assessment of probabilities that the true values fall within certain ranges, adding yet another probabilistic or chance component to the evaluation of the situation.

The difficulty of incorporating multiple, interacting, probabilistic processes into a model that can utilize uncertain data has prevented (to date) development of analytical models (mathematical equations developed from theory) which encompass more than a small subset of the processes known to affect

wildlife population dynamics. It is possible that the mental models of some biologists are sufficiently complex to predict accurately population vulnerabilities to extinction under a range of conditions, but it is not possible to assess objectively the precision of such intuitive assessments, and it is difficult to transfer that knowledge to others who need also to evaluate the situation. Computer simulation models have increasingly been used to assist in PVA. Although rarely as elegant as models framed in analytical equations, computer simulation models can be well suited for the complex task of evaluating risks of extinction. Simulation models can include as many factors that influence population dynamics as the modeler and the user of the model want to assess. Interactions between processes can be modeled, if the nature of those interactions can be specified. Probabilistic events can be easily simulated by computer programs, providing output that gives both the mean expected result and the range or distribution of possible outcomes. In theory, simulation programs can be used to build models of population dynamics that include all the knowledge of the system which is available to experts. In practice, the models will be simpler, because some factors are judged unlikely to be important, and because the persons who developed the model did not have access to the full array of expert knowledge.

Although computer simulation models can be complex and confusing, they are precisely defined and all the assumptions and algorithms can be examined. Therefore, the models are objective, testable, and open to challenge and improvement. PVA models allow use of all available data on the biology of the taxon, facilitate testing of the effects of unknown or uncertain data, and expedite the comparison of the likely results of various possible management options.

PVA models also have weaknesses and limitations. A model of the population dynamics does not define the goals for conservation planning. Goals, in terms of population growth, probability of persistence, number of extant populations, genetic diversity, or other measures of population performance must be defined by the management authorities before the results of population modeling can be used. Because the models incorporate many factors, the number of possibilities to test can seem endless, and it can be difficult to determine which of the factors that were analyzed are most important to the population dynamics. PVA models are necessarily incomplete. We can model only those factors which we understand and for which we can specify the parameters. Therefore, it is important to realize that the models probably underestimate the threats facing the population. Finally, the models are used to predict the long-term effects of the processes presently acting on the population. Many aspects of the situation could change radically within the time span that is modeled. Therefore, it is important to reassess the data and model results periodically, with changes made to the conservation programs as needed.

Dealing with uncertainty

It is important to recognize that uncertainty regarding the biological parameters of a population and its consequent fate occurs at several levels and for independent reasons. Uncertainty can occur because the parameters have never been measured on the population. Uncertainty can occur because limited field data have yielded estimates with potentially large sampling error. Uncertainty can occur because independent studies have generated discordant estimates. Uncertainty can occur because environmental conditions or population status have been changing over time, and field surveys were conducted during periods which may not be representative of long-term averages. Uncertainty can occur because the environment will change in the future, so that measurements made in the past may not accurately predict future conditions.

Sensitivity testing is necessary to determine the extent to which uncertainty in input parameters results in uncertainty regarding the future fate of the population. If alternative plausible parameter values result in divergent predictions for the population, then it is important to try to resolve the uncertainty with better data. Sensitivity of population dynamics to certain parameters also indicates that those parameters describe factors that could be critical determinants of population viability. Such factors are therefore good candidates for efficient management actions designed to ensure the persistence of the population.

The above kinds of uncertainty should be distinguished from several more sources of uncertainty about the future of the population. Even if long-term average demographic rates are known with precision, variation over time caused by fluctuating environmental conditions will cause uncertainty in the fate of the population at any given time in the future. Such environmental variation should be incorporated into the model used to assess population dynamics, and will generate a range of possible outcomes (perhaps represented as a mean and standard deviation) from the model. In addition, most biological processes are inherently stochastic, having a random component. The stochastic or probabilistic nature of survival, sex determination, transmission of genes, acquisition of mates, reproduction, and other processes preclude exact determination of the future state of a population. Such demographic stochasticity should also be incorporated into a population model, because such variability both increases our uncertainty about the future and can also change the expected or mean outcome relative to that which would result if there were no such variation. Finally, there is "uncertainty" which represents the alternative actions or interventions that might be pursued as a management strategy. The likely effectiveness of such management options can be explored by testing alternative scenarios in the model of population dynamics, in much the same way that sensitivity testing is used to explore the effects of uncertain biological parameters.

Often, the uncertainty regarding a number of aspects of the population biology, current status, and threats to persistence is too large to allow scientifically accurate and reliable projections of population dynamics. Therefore, the predictions made from PVA models should be considered to be projections about what would most likely happen to the population *if* various hypotheses about the status of the populations and the threats are true. Conservation and management decisions must be made based on the most plausible hypotheses about the population status, before sufficient data could be collected to test those hypotheses scientifically. An important advantage of PVA models is that they forced systematic consideration and specification of the assumptions and hypotheses that must be made in the absence of adequate data. This facilitates careful reassessment and improvement in the analyses, as better data become available.

Questions that can be explored with PVA models

Below are some of the conservation and management questions that can be explored by Population Viability Analysis modeling. References describing uses of *VORTEX* give many examples of these and other applications of PVA techniques to guide conservation.

Using the best current information on the biology of the taxon and its habitat, are the populations projected to persist if conditions remain as they are now? Beyond just the persistence of the population, what is the most likely average population size, range of population sizes across years, and rate of loss of genetic variation? If the population is at risk of extinction, is the extinction expected to result primarily from negative average population growth (mean deaths exceeding mean births), from large fluctuations in numbers, from effects of accumulated inbreeding, or from a combination of these factors?

Given that there is considerable uncertainty about several aspects of the species biology and its habitat, is the population likely to persist across the plausible ranges of parameters that might characterize the population? In particular, how sensitive are the population dynamics to varying estimates of reproductive success, juvenile survival, adult survival, effects of natural catastrophes, initial population size, carrying capacity of the habitat, and dispersal among populations? Are there critical values for any of these parameters which demarcate a transition from a population that would be considered viable to one that is not?

Which factors have the greatest influence on the projected population performance? If important factors are identified, management actions might be designed to improve these factors or ameliorate the negative effects. How much change would be required in aspects of the population in order to ensure population survival?

What would be the effect of removing some individuals from the population? Would there be a significant benefit from supplementing the population with individuals translocated from other populations or released from captive breeding stocks? Can the population sustain controlled harvest? Can it sustain poaching?

Would a corridor connecting fragmented habitats improve long-term viability? Could the same effect be achieved by translocating a few individuals? What will happen to population viability if mortality increases for individuals dispersing between habitat patches?

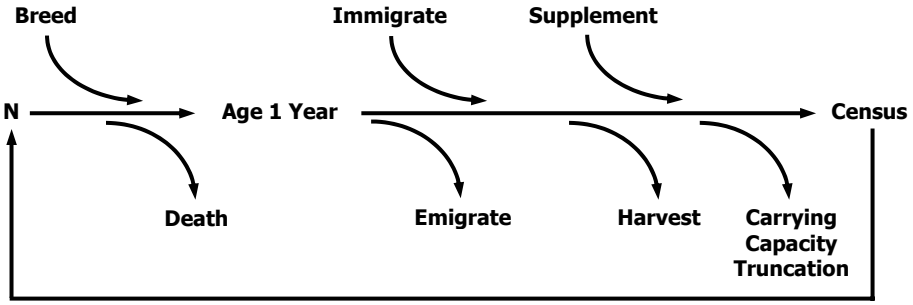
What will happen to the wildlife population if trends in human populations and human impacts on the environment continue unabated?

The *VORTEX* Population Viability Analysis Model

The *VORTEX* computer program is a simulation of the effects of deterministic forces as well as demographic, environmental and genetic stochastic events on wildlife populations. It is an attempt to model many of the extinction vortices that can threaten persistence of small populations (hence, its name). *VORTEX* models population dynamics as discrete, sequential events that occur according to probabilities that are random variables following user-specified distributions. *VORTEX* simulates a population by stepping through a series of events that describe an annual cycle of a typical sexually reproducing, diploid organism: mate selection, reproduction, mortality, increment of age by one year, migration among populations, removals, supplementation, and then truncation (if necessary) to the carrying capacity. Although *VORTEX* simulates life events on an annual cycle, a user could model "years" that are other than 12 months duration. The simulation of the population is iterated many times to generate the distribution of fates that the population might experience.

VORTEX is an individual-based model. That is, it creates a representation of each animal in its memory and follows the fate of the animal through each year of its lifetime. *VORTEX* keeps track of the sex, age, and parentage of each animal. Demographic events (birth, sex determination, mating, dispersal, and death) are modeled by determining for each animal in each year of the simulation whether any of the events occur. (See figure below.)

VORTEX Simulation Model Timeline



Events listed above the timeline increase N, while events listed below the timeline decrease N.

VORTEX requires a lot of population-specific data. For example, the user must specify the amount of annual variation in each demographic rate caused by fluctuations in the environment. In addition, the frequency of each type of catastrophe (drought, flood, epidemic disease) and the effects of the

catastrophes on survival and reproduction must be specified. Rates of migration (dispersal) between each pair of local populations must be specified. Because *VORTEX* requires specification of many biological parameters, it is not necessarily a good model for the examination of population dynamics that would result from some generalized life history. It is most usefully applied to the analysis of a specific population in a specific environment.

In the program explanation that follows, demographic rates are described as constants specified by the user. Although this is the way the program is most commonly and easily used, *VORTEX* does provide the capability to specify most demographic rates as functions of time, density, and other parameters (see Chapter 5).

Demographic stochasticity

VORTEX models demographic stochasticity by determining the occurrence of probabilistic events such as reproduction, litter size, sex determination, and death with a pseudo-random number generator. For each life event, if the random value sampled from a specified distribution falls above the user-specified probability, the event is deemed to have occurred, thereby simulating a binomial process. Demographic stochasticity is therefore a consequence of the uncertainty regarding whether each demographic event occurs for any given animal.

The source code used to generate random numbers uniformly distributed between 0 and 1 was obtained from Maier (1991), based on the algorithm of Kirkpatrick and Stoll (1981). Random deviates from binomial distributions, with mean p and standard deviation s, are obtained by first determining the integral number of binomial trials, N, that would produce the value of s closest to the specified value, according to:

$$N = \frac{p(1-p)}{s^2}$$

N binomial trials are then simulated by sampling from the uniform 0-1 distribution to obtain the desired result, the frequency or proportion of successes. If the value of N determined for a desired binomial distribution is larger than 25, a normal approximation is used in place of the binomial distribution. This normal approximation must be truncated at 0 and at 1 to allow use in defining probabilities, although, with such large values of N, s is small relative to p and the truncation would be invoked only rarely. To avoid introducing bias with this truncation, the normal approximation to the binomial (when used) is truncated symmetrically around the mean. The algorithm for generating random numbers from a unit normal distribution follows Latour (1986).

Environmental variation

VORTEX can model annual fluctuations in birth and death rates and in carrying capacity as might result from environmental variation. To model environmental variation, each demographic parameter is assigned a distribution with a mean and standard deviation that is specified by the user. Annual fluctuations in probabilities of reproduction and mortality are modeled as binomial distributions. Environmental variation in carrying capacity is modeled as a normal distribution. Environmental variation in demographic rates can be correlated among populations.

Catastrophes

Catastrophes are modeled in *VORTEX* as random events that occur with specified probabilities. A catastrophe will occur if a randomly generated number between zero and one is less than the probability

of occurrence. Following a catastrophic event, the chances of survival and successful breeding for that simulated year are multiplied by severity factors. For example, forest fires might occur once in 50 years, on average, killing 25% of animals, and reducing breeding by survivors 50% for the year. Such a catastrophe would be modeled as a random event with 0.02 probability of occurrence each year, and severity factors of 0.75 for survival and 0.50 for reproduction. Catastrophes can be local (impacting populations independently), or regional (affecting sets of populations simultaneously).

Genetic processes

VORTEX models loss of genetic variation in populations, by simulating the transmission of alleles from parents to offspring at a hypothetical neutral (non-selected) genetic locus. Each animal at the start of the simulation is assigned two unique alleles at the locus. Each offspring created during the simulation is randomly assigned one of the alleles from each parent. *VORTEX* monitors how many of the original alleles remain within the population, and the average heterozygosity and gene diversity (or "expected heterozygosity") relative to the starting levels. *VORTEX* also monitors the inbreeding coefficients of each animal, and can reduce the juvenile survival of inbred animals to model the effects of inbreeding depression.

Inbreeding depression is modeled as a loss of viability of inbred animals during their first year. The severity of inbreeding depression is commonly measured by the number of "lethal equivalents" in a population (Morton et al. 1956). The number of lethal equivalents per diploid genome estimates the average number of lethal alleles per individual in the population if all deleterious effects of inbreeding were due entirely to recessive lethal alleles. A population in which inbreeding depression is one lethal equivalent per diploid genome may have one recessive lethal allele per individual, it may have two recessive alleles per individual, each of which confer a 50% decrease in survival, or it may have some other combination of recessive deleterious alleles which equate in effect with one lethal allele per individual.

VORTEX partitions the total effect of inbreeding (the total lethal equivalents) into an effect due to recessive lethal alleles and an effect due to loci at which there is heterozygote advantage (superior fitness of heterozygotes relative to all homozygote genotypes). To model the effects of lethal alleles, each founder starts with a unique recessive lethal allele (and a dominant non-lethal allele) at up to five modeled loci. By virtue of the deaths of individuals that are homozygous for lethal alleles, such alleles can be removed slowly by natural selection during the generations of a simulation. This diminishes the probability that inbred individuals in subsequent generations will be homozygous for a lethal allele.

Heterozygote advantage is modeled by specifying that juvenile survival is related to inbreeding according to the logarithmic model:

$$\ln(S) = A - BF$$

in which S is survival, F is the inbreeding coefficient, A is the logarithm of survival in the absence of inbreeding, and B is the portion of the lethal equivalents per haploid genome that is due to heterozygote advantage rather than to recessive lethal alleles. Unlike the situation with fully recessive deleterious alleles, natural selection does not remove deleterious alleles at loci in which the heterozygote has higher fitness than both homozygotes, because all alleles are deleterious when homozygous and beneficial when present in heterozygous combination with other alleles. Thus, under heterozygote advantage, the impact of inbreeding on survival does not diminish during repeated generations of inbreeding. Unfortunately, for relatively few species are data available to allow estimation of the effects of inbreeding, and the magnitude of these effects apparently varies considerably among species (Falconer 1981; Ralls et al. 1988; Lacy et al. 1993) and even among populations of the same species (Lacy et al. 1996). Even without detailed pedigree data from which to estimate the number of lethal equivalents in a

population and the underlying nature of the genetic load (recessive alleles or heterozygote advantage), PVAs must make assumptions about the effects of inbreeding on the population being studied. If genetic effects are ignored, the PVA will overestimate the viability of small populations. In some cases, it might be considered appropriate to assume that an inadequately studied species would respond to inbreeding in accord with the median (3.14 lethal equivalents per diploid) reported in the survey by Ralls et al. (1988). In other cases, there might be reason to make more optimistic assumptions (perhaps the lower quartile, 0.90 lethal equivalents), or more pessimistic assumptions (perhaps the upper quartile, 5.62 lethal equivalents). In the few species in which inbreeding depression has been studied carefully, about half of the effects of inbreeding are due recessive lethal alleles and about half of the effects are due to heterozygote advantage or other genetic mechanisms that are not diminished by natural selection during generations of inbreeding, although the proportion of the total inbreeding effect can vary substantially among populations (Lacy and Ballou 1998).

A full explanation of the genetic mechanisms of inbreeding depression is beyond the scope of this manual, and interested readers are encouraged to refer to the references cited above.

VORTEX can model monogamous or polygamous mating systems. In a monogamous system, a relative scarcity of breeding males may limit reproduction by females. In polygamous or monogamous models, the user can specify the proportion of the adult males in the breeding pool. Males are randomly reassigned to the breeding pool each year of the simulation, and all males in the breeding pool have an equal chance of siring offspring.

Deterministic processes

VORTEX can incorporate several deterministic processes, in addition to mean age-specific birth and death rates. Density dependence in mortality is modeled by specifying a carrying capacity of the habitat. When the population size exceeds the carrying capacity, additional morality is imposed across all age classes to bring the population back down to the carrying capacity. Each animal in the population has an equal probability of being removed by this truncation. The carrying capacity can be specified to change over time, to model losses or gains in the amount or quality of habitat.

Density dependence in reproduction is modeled by specifying the proportion of adult females breeding each year as a function of the population size. The default functional relationship between breeding and density allows entry of Allee effects (reduction in breeding at low density) and/or reduced breeding at high densities.

Populations can be supplemented or harvested for any number of years in each simulation. Harvest may be culling or removal of animals for translocation to another (unmodeled) population. The numbers of additions and removals are specified according to the age and sex of animals.

Migration among populations

VORTEX can model up to 50 populations, with possibly distinct population parameters. Each pairwise migration rate is specified as the probability of an individual moving from one population to another. Migration among populations can be restricted to one sex and/or a limited age cohort. Emigration from a population can be restricted to occur only when the number of animals in the population exceeds a specified proportion of the carrying capacity. Dispersal mortality can be specified as a probability of death for any migrating animal, which is in addition to age-sex specific mortality. Because of between-population migration and managed supplementation, populations can be recolonized. *VORTEX* tracks the dynamics of local extinctions and recolonizations through the simulation.

Output

VORTEX outputs: **(1)** probability of extinction at specified intervals (e.g., every 10 years during a 100 year simulation), **(2)** median time to extinction, if the population went extinct in at least 50% of the simulations, **(3)** mean time to extinction of those simulated populations that became extinct, and **(4)** mean size of, and genetic variation within, extant populations.

Standard deviations across simulations and standard errors of the mean are reported for population size and the measures of genetic variation. Under the assumption that extinction of independently replicated populations is a binomial process, the standard error of the probability of extinction is reported by *VORTEX* as:

$$\mathrm{SE}(p) = \sqrt{\frac{p(1-p)}{n}}$$

in which the frequency of extinction was p over n simulated populations. Demographic and genetic statistics are calculated and reported for each subpopulation and for the metapopulation.

Sequence of program flow

(1) The seed for the random number generator is initialized with the number of seconds elapsed since the beginning of the 20th century.

(2) The user is prompted for an output file name, duration of the simulation, number of iterations, the size below which a population is considered extinct, and a large number of population parameters.

(3) The maximum allowable population size (necessary for preventing memory overflow) is calculated as:

$$K_{\max} = (K + 3s)(1 + L)$$

in which K is the maximum carrying capacity (carrying capacity can be specified to change during a simulation, so the maximum carrying capacity can be greater than the initial carrying capacity), s is the annual environmental variation in the carrying capacity expressed as a standard deviation, and L is the specified maximum litter size.

(4) Memory is allocated for data arrays. If insufficient memory is available for data arrays then N_{max} is adjusted downward to the size that can be accommodated within the available memory and a warning message is given. In this case it is possible that the analysis may have to be terminated because the simulated population exceeds N_{max}. Because N_{max} is often several-fold greater than the likely maximum population size in a simulation, a warning that it has been adjusted downward because of limiting memory often will not hamper the analyses.

(5) The deterministic growth rate of the population is calculated from mean birth and death rates that have been entered. Algorithms follow cohort life-table analyses (Ricklefs 1979). Generation time and the expected stable age distribution are also calculated. Life-table calculations assume constant birth and death rates, no limitation by carrying capacity, no limitation of mates, no loss of fitness due to inbreeding depression, and that the population is at the stable age distribution. The effects of catastrophes are incorporated into the life table analysis by using birth and death rates that are weighted averages of the values in years with and without catastrophes, weighted by the probability of a catastrophe occurring or not occurring.

(6) Iterative simulation of the population proceeds via steps 7 through 26 below.

(7) The starting population is assigned an age and sex structure. The user can specify the exact age-sex structure of the starting population, or can specify an initial population size and request that the population be distributed according to the stable age distribution calculated from the life table. Individuals in the starting population are assumed to be unrelated. Thus, inbreeding can occur only in second and later generations.

(8) Two unique alleles at a hypothetical neutral genetic locus are assigned to each individual in the starting population and to each individual supplemented to the population during the simulation. *VORTEX* therefore uses an infinite alleles model of genetic variation. The subsequent fate of genetic variation is tracked by reporting the number of extant neutral alleles each year, the expected heterozygosity or gene diversity, and the observed heterozygosity. The expected heterozygosity, derived from the Hardy-Weinberg equilibrium, is given by

$$H_e = 1 - \sum \left(p_i^2 \right)$$

in which p_i is the frequency of allele i in the population. The observed heterozygosity is simply the proportion of the individuals in the simulated population that are heterozygous. Because of the starting assumption of two unique alleles per founder, the initial population has an observed heterozygosity of 1.0 at the hypothetical locus and only inbred animals can become homozygous. Proportional loss of heterozygosity through random genetic drift is independent of the initial heterozygosity and allele frequencies of a population (Crow and Kimura 1970), so the expected heterozygosity remaining in a simulated population is a useful metric of genetic decay for comparison across scenarios and populations. The mean observed heterozygosity reported by *VORTEX* is the mean inbreeding coefficient of the population.

(9) For each of the10 alleles at five non-neutral loci that are used to model inbreeding depression, each founder is assigned a unique lethal allele with probability equal to 0.1 x the mean number of lethal alleles per individual.

(10) Years are iterated via steps 11 through 25 below.

(11) The probabilities of females producing each possible size litter are adjusted to account for density dependence of reproduction (if any).

(12) Birth rate, survival rates, and carrying capacity for the year are adjusted to model environmental variation. Environmental variation is assumed to follow binomial distributions for birth and death rates and a normal distribution for carrying capacity, with mean rates and standard deviations specified by the user. At the outset of each year a random number is drawn from the specified binomial distribution to determine the percent of females producing litters. The distribution of litter sizes among those females that do breed is maintained constant. Another random number is drawn from a specified binomial distribution to model the environmental variation in mortality rates. If environmental variations in reproduction and mortality are chosen to be correlated, the random number used to specify mortality rates for the year is chosen to be the same percentile of its binomial distribution as was the number used to specify reproductive rate. Otherwise, a new random number is drawn to specify the deviation of age- and sex-specific mortality rates from their means. Environmental variation across years in mortality rates is always forced to be correlated among age and sex classes.

The carrying capacity (K) for the year is determined by first increasing or decreasing the carrying capacity at year 1 by an amount specified by the user to account for changes over time.

Environmental variation in K is then imposed by drawing a random number from a normal distribution with the specified values for mean and standard deviation.

(13) Birth rates and survival rates for the year are adjusted to model any catastrophes determined to have occurred in that year.

(14) Breeding males are selected for the year. A male of breeding age is placed into the pool of potential breeders for that year if a random number drawn for that male is less than the proportion of adult males specified to be breeding. Breeding males are selected independently each year; there is no long-term tenure of breeding males and no long-term pair bonds.

(15) For each female of breeding age, a mate is drawn at random from the pool of breeding males for that year. If the user specifies that the breeding system is monogamous, then each male can only be paired with a single female each year. Males are paired only with those females which have already been selected for breeding that year. Thus, males will not be the limiting sex unless there are insufficient males to pair with the successfully breeding females.

If the breeding system is polygynous, then a male may be selected as the mate for several females. The degree of polygyny is determined by the proportion of males in the pool of potential breeders each year.

The size of the litter produced by that pair is determined by comparing the probabilities of each potential litter size (including litter size of 0, no breeding) to a randomly drawn number. The offspring are produced and assigned a sex by comparison of a random number to the specified birth sex ratio. Offspring are assigned, at random, one allele at the hypothetical genetic locus from each parent.

(16) The genetic kinship of each new offspring to each other living animal in the population is determined. The kinship between new animal A, and another existing animal, B, is

$$f_{AB} = 0.5(f_{MB} + f_{PB})$$

in which f_{ij} is the kinship between animals i and j, M is the mother of A, and P is the father of A. The inbreeding coefficient of each animal is equal to the kinship between its parents, $F = f_{MP}$, and the kinship of an animal to itself is $f_A = 0.5(1 + F)$. (See Ballou 1983 for a detailed description of this method for calculating inbreeding coefficients.)

(17) The survival of each animal is determined by comparing a random number to the survival probability for that animal. In the absence of inbreeding depression, the survival probability is given by the age and sex-specific survival rate for that year. If a newborn individual is homozygous for a lethal allele, it is killed. Otherwise, the survival probability for individuals in their first year is multiplied by

$$e^{-b(1-\Pr[Lethals])F}$$

in which b is the number of lethal equivalents per haploid genome, and Pr[*Lethals*] is the proportion of this inbreeding effect due to lethal alleles.

(18) The age of each animal is incremented by 1.

(19) If more than one population is being modeled, migration among populations occurs stochastically with specified probabilities.

(20) If population harvest is to occur that year, the number of harvested individuals of each age and sex class are chosen at random from those available and removed. If the number to be removed do not exist for an age-sex class, *VORTEX* continues but reports that harvest was incomplete.

(21) Dead animals are removed from the computer memory to make space for future generations.

(22) If population supplementation is to occur in a particular year, new individuals of the specified age-class are created. Each immigrant is assumed to be genetically unrelated to all other individuals in the population, and it carries the number of lethal alleles that was specified for the starting population.

(23) The population growth rate is calculated as the ratio of the population size in the current year to the previous year.

(24) If the population size (N) exceeds the carrying capacity (K) for that year, additional mortality is imposed across all age and sex classes. The probability of each animal dying during this carrying capacity truncation is set to $(N - K)/N$, so that the expected population size after the additional mortality is K.

(25) Summary statistics on population size and genetic variation are tallied and reported.

(26) Final population size and genetic variation are determined for the simulation.

(27) Summary statistics on population size, genetic variation, probability of extinction, and mean population growth rate are calculated across iterations and output.

Appendix

II

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Appendix

III

VORTEX Bibliography

We have attempted to compile an exhaustive list of articles and reports that use *VORTEX* as a tool in population viability analysis. If we have missed any other examples, or if you have published a contribution that you would like to add to the growing list, please contact the Conservation Breeding Specialist Group (see page 3 for details) and we will update this *Bibliography*.

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Appendix

IV

Reprints

Lacy, R.C. 2000. Structure of the VORTEX simulation model for population viability analysis. Ecological Bulletins 48:191-203.

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Lacy, R.C. 2000. Considering threats to the viability of small populations using individual-based models. Ecological Bulletins 48:39-51.

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Ecological Bulletins 48: 191–203. Copenhagen 2000

Structure of the VORTEX simulation model for population viability analysis

Robert C. Lacy

Lacy, R. C. 2000. Structure of the VORTEX simulation model for population viability analysis. – Ecol. Bull. 48: 191–203.

The structure of the VORTEX computer simulation model for population viability analysis is outlined. The program flow is described here in order to provide a detailed specification of the structure of a widely used population viability analysis model. VORTEX is an individual-based simulation program that models the effects of mean demographic rates, demographic stochasticity, environmental variation in demographic rates, catastrophes, inbreeding depression, harvest and supplementation, and metapopulation structure on the viability of wildlife populations. The model facilitates analysis of density-dependent reproduction and changing habitat availability, and most demographic rates can optionally be specified as flexible functions of density, time, population gene diversity, inbreeding, age, and sex. VORTEX projects changes in population size, age and sex structure, and genetic variation, as well as estimating probabilities and times to extinction and recolonization.

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"VORTEX and like programs do exactly what they are told to do, as constrained by the static single-species models that provide their structure. They can be useful for various purposes so long as the user understands what the programs are doing ..." (Caughley and Gunn 1996, p. 208).

The complexity and multiplicity of processes influencing the dynamics of natural populations of animals and plants means that population viability analysis (PVA) models are also frequently complex. Different models incorporate different population processes. Individual population processes can be modeled in various ways, requiring different sets of driving variables, using different equations to define the processes, and providing different output to describe the population dynamics. Users of PVA models should understand the basic structure of the models they use, and it is important that models used for scientific studies and conservation efforts can be examined and replicated. Yet often the details of PVA computer programs are not available to the users, because the code is proprietary information or otherwise not provided to users, or simply because the task of reading and understanding the source code for large and complex programs is formidable.

One possible remedy to the problem of PVA users needing to understand the models being used is for practitioners to develop their own computer programs. This would result in the user having a full understanding of a model that would be specifically designed for the analysis. Development of user-specific and case-specific models is usually not practical, however, as many population biologists are not skilled computer programmers, and the time required to develop a complex model is often prohibitive. Moreover, a complex computer program developed by and used by one person will sometimes contain serious programming errors. The testing of programs that are widely used may be a necessary prerequisite for reliable population viability analyses to be employed effectively in biodi-

versity conservation. Finally, the flexibility and expansive capabilities of generic PVA software to model a large diversity of population processes will often lead PVA practitioners to consider threats to population viability that would otherwise have been neglected.

Widely available PVA software can serve the same role as do statistical analysis packages. The ease of use, flexible application to diverse needs, and extensive prior testing facilitate many applications that would not otherwise be attempted. Ideally, perhaps, all users of statistical methods would write their own programs or otherwise study the code of the software entrusted for the analyses. More practically, confidence is gained in the reliability of generic software tools as more people use the programs and compare the generated results to expectations from statistical theory and to results for simple and well known cases. Also, users of statistical software are expected to be sufficiently familiar with the methods of statistical analysis to be able to choose appropriate models to apply to their problem, to be able to provide the proper input, and to be able to interpret the results.

Unlike the situation for statistical methods, however, there are not yet widely accepted and published accounts of standard methods for population viability analysis. The methods of population-based models (e.g., Starfield and Bleloch 1986, Burgman et al. 1993) are extensions of the methods of population ecology and demography (e.g., Pielou 1977, Caswell 1989), but many details of model construction require decisions about algorithms and methods that are not fully delineated in general treatments. The methods of individual-based PVA models have been only cursorily described in the scientific literature. Below is an outline of one widely used PVA software package, VORTEX, ver. 8.20. The basic approach taken in the VORTEX model is described in Lacy (1993), in Lindenmayer et al. (2000) and other papers describing applications of VORTEX, and in the software manual (Miller and Lacy 1999). Detailed documentation of the program flow and algorithms is provided here, so that users of VORTEX can confirm that the model is performing the analyses that are intended, and so that PVA practitioners in general can see an example of the structure of an individual-based PVA model. The VORTEX program is available at http://www2.netcom.com/~rlacy/vortex.html.

The pseudo-code presented below is an English-language outline of the program flow and primary algorithms used by VORTEX (which is written in the C programming language). This pseudo-code omits coding for: 1) input routines for reading parameters from files and/or keyboard; 2) output routines for writing results to files; 3) specification of default parameter values; 4) checks for illegal values, error handling; 5) memory management and initialization of memory; 6) details of C coding to achieve algorithms; 7) routines for on-line help; 8) routines for graphical display of functions specifying demographic rates, population sizes during simulations, simulation results; 9) routines for evaluating equations that specify demographic rates (e.g., breeding, mortality) as functions of population and individual variables (e.g., population size, gene diversity, year, age, sex, inbreeding) (see note 3 below); 10) tallies of mean within-population statistics and metapopulation summaries; 11) algorithms for calculating basic statistics, such as means, standard deviations, standard errors, and medians across years and across iterations.

Variables for storing input, intermediate calculations, and output are indicated in the pseudo-code by italicized labels. Many of the variables are arrays (e.g., a value stored for each population, or for each age class, or for each individual), as suggested by the loops within which they are calculated and used. The indices of such arrays are indicated within brackets (e.g., *MortalityRate[p][s][x]*, for each population, *p*, sex, *s*, and age, *x*). VORTEX uses many more variables (not shown in the pseudo-code) for facilitating calculations and accumulating sums, sums of squares, and other components needed for the basic statistics reported in the output.

In the pseudo-code, loops are indicated with FOR: and END LOOP statements, or by WHILE: and END WHILE statements. Conditional actions are indicated by IF: and END IF statements, or by IF:, ELSE:, and END IF/ELSE statements. BREAK indicates that program flow exits from the bottom of a loop. CONTINUE indicates that program flow jumps back to the next value at the top of the loop. Multiplication is indicated by the asterisk (*) symbol; ^ indicates exponentiation; SQRT indicates the positive square root.

Function modules defined outside of the main body of the pseudo-code program are labeled in the form **FUNCTION()**, and are specified below the main **VORTEX()** program. The actual C code is subdivided into many smaller functions; the pseudo-code shows only the flow of the overall program and its largest modules. The functions **RAND()** and **NRAND()** indicate, respectively, that a random number is generated from the uniform 0-1 distribution or from a unit normal distribution.

Explanatory comments, following pseudo-code sections, are preceded by //. More extensive explanations are given in notes following the code.

As an individual-based PVA simulation model, VORTEX represents each individual in memory, simulates life events (such as sex determination, breeding, mortality, and dispersal) which could occur to each individual, and monitors the status of each individual and the population as a whole. The characteristics tracked for each animal are: sex, alive/dead status, population membership, age, inbreeding coefficient, and two alleles at each of six loci. In addition, VORTEX maintains a matrix of kinship coefficients between all pairs of living animals, as this provides inbreeding coefficients for any offspring.

VORTEX models changes to a population as a series of discrete events that occur once per year (or other time interval). The annual sequence of demographic events is:

breeding; mortality; age 1 yr; migrate (disperse) among populations; harvest (managed removals); supplementation (managed additions); carrying capacity truncation; census (Fig. 1). Occurrences of events are probabilistic; demographic stochasticity emerges from chance variation in which individuals breed, die, and are of each sex. Environmental variation in demographic rates is imposed by sampling rates from specified distributions during each simulated year. Catastrophes, which occur with specified probabilities, cause one-year reductions in reproduction and survival. Genetic effects are modeled as reduced survivorship of inbred individuals.

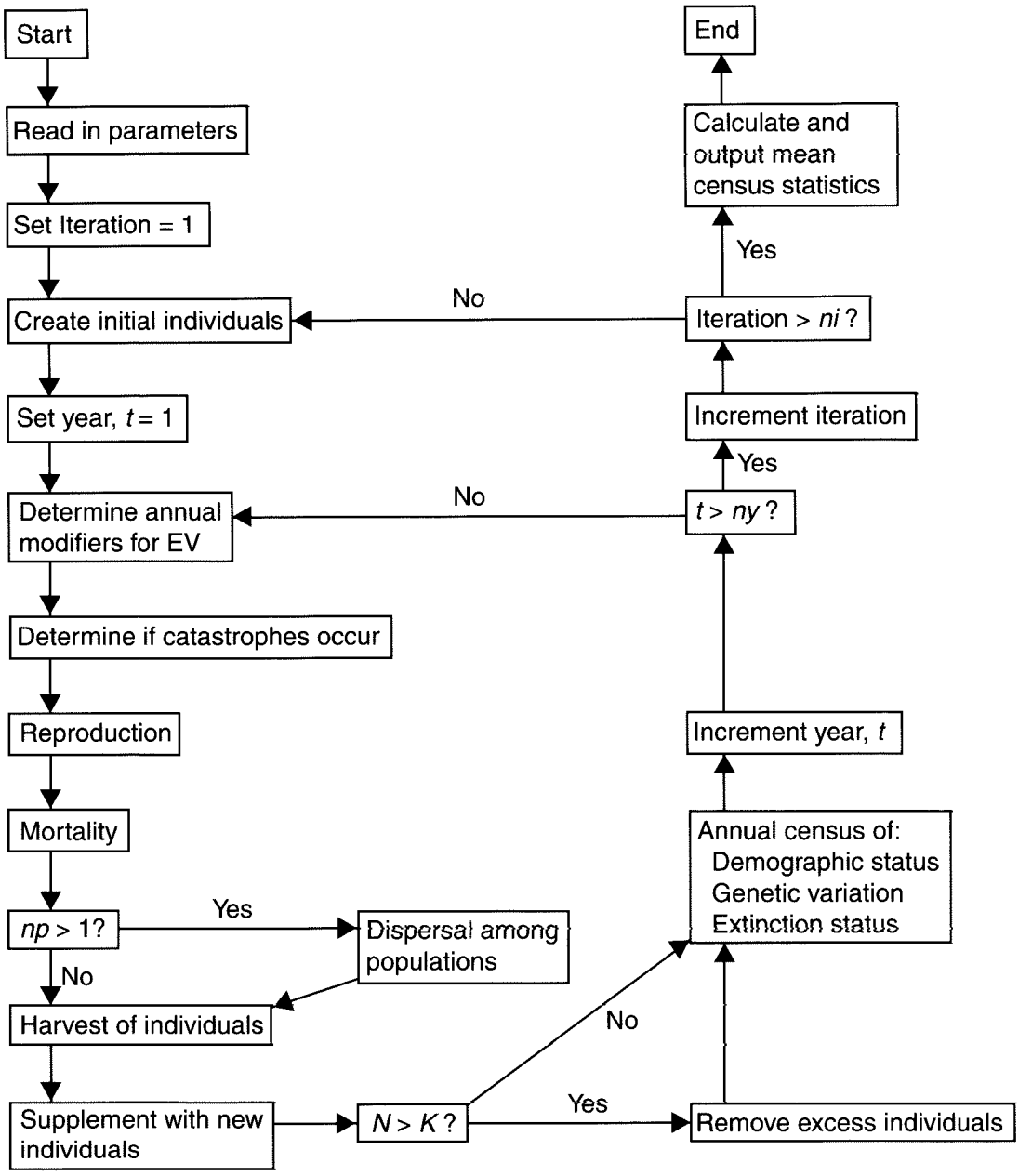

Fig. 1. Flow chart of the primary components of the Vortex simulation. Each step from "Create initial individuals" through "Annual census" is applied to each population in a modeled metapopulation. t = year; ny = number of years simulated; np = number of populations; ni = number of iterations; N = population size; K = carrying capacity; EV = environmental variation.

VORTEX program pseudo-code

```
BEGIN PROGRAM VORTEX():
Initialize random number generator; // See Note 1.
   FOR (each scenario):
      READ_SPECIES_PARAMETERS();
      IF (NumberOfPopulations > 1):
         READ_MIGRATION_PARAMETERS();
// VORTEX describes dispersal between populations as "migration."
      END IF
      FOR (each population, p):
         READ_POPULATION_PARAMETERS(p);
      END (population) LOOP
      FOR (each population, pSource):
// Calculate cumulative migration rates for each pairwise transition between populations.
         Set CumMigrationProb[pSource][1] = MigrationProb[pSource][1];
         FOR (each destination population, pDestination, greater than 1):
            Set CumMigrationProb[pSource][pDestination] = CumMigrationProb[pSource][pDestination -1]+ MigrationProb[pSource][pDestination];
         END (pDestination) LOOP
      END (pSource) LOOP
      Set NumberLethals = InbreedingGeneticLoad * ProportionLoadDueToLethals;
      Set LethalEquivalents = InbreedingGeneticLoad * (1 - ProportionLoadDueToLethals);
// See Note 2.
      FOR (each population, p):
         Set GlobalBreedEV[p] = BreedEV[p] * EVConcordanceAmongPopulations;
         Set LocalBreedEV[p] = SQRT( BreedEV[p] ^2 – GlobalBreedEV[p] ^2);
// Partition Environmental Variation in breeding (BreedEV) into the component that is common to all populations (GlobalBreedEV) and the component that is specific to each population. (LocalBreedEV); TotalEV ^ 2 = GlobalEV ^ 2 + LocalEV ^2
// Note: EVs are given as standard deviations.
         FOR (each sex, s):
            FOR (each age, x, up to age of breeding):
               Set GlobalMortEV[p][s][x] = MortEV[p][s][x] * EVConcordanceAmongPopulations;
               Set LocalMortEV[p][s][x] = SQRT(MortEV[p][s][x] ^2 – GlobalMortEV[p][s][x] ^2);
// Partition EV in mortality (MortEV) into the component that is common to all populations (GlobalMortEV) and the component that is specific to each population (LocalMortEV).
            END (age) LOOP
         END (sex) LOOP
         Set GlobalKEV[p] = KEV[p] * EVConcordanceAmongPopulations;
         Set LocalKEV[p] = SQRT( KEV[p] ^2 – GlobalKEV[p] ^2);
// Partition EV in carrying capacity (KEV) into the component that is common to all populations (GlobalKEV) and the component that is specific to each population (LocalKEV).
      END (population) LOOP
      FOR (each iteration):
         FOR (each population):
            Create initial individuals, assigning population, sex, age, alive/dead status, inbreeding coefficient and kinships (initially 0), and alleles at six loci;
            FOR (each of five non-neutral loci, l):
               FOR (each founder allele, a):
// The probability that a given founder allele is a lethal is NumberLethals / 10, because there are 10 alleles across the five diploid loci.
                  IF (RAND() < NumberLethals / 10):
                     Set Lethal[l][a] = TRUE;
// Allele, a, of locus, l, is a recessive lethal.
                  ELSE:
                     Set Lethal[l][a] = FALSE;
                  END IF/ELSE
               END (founder allele) LOOP
            END (locus) LOOP
            Display initial population sizes on screen and write to output files;
         END (population) LOOP
         FOR (each year):
            IF (NumberPopulations > 1):
               GLOBAL_EV_RANDS();
// Generate random numbers for specifying environmental variation, concordant across populations, for the year.
            END (NumberPopulations) IF
            FOR (each population, p):
               LOCAL_EV_RANDS();
               CATASTROPHES(p);
// Determine if catastrophes occur that year.
               Determine carrying Capacity (K) for year;
// See Note 3.
               Add LocalKEVNRand * LocalKEV[p] to CarryingCapacity[p];
// Adjust K for local EV.
               Add GlobalKEVNRand * GlobalKEV[p] to CarryingCapacity[p];
// Adjust K for global EV.
               BREED(p);
// Go through breeding cycle to produce offspring.
               MORTALITY(p);
// Determine who dies that year.
            END (population) LOOP
            Add 1 to the age of each animal;
            IF (NumberPopulations > 1):
               MIGRATE();
```

```
// Determine which animals migrate between populations.
            END IF
            FOR (each population, p):
               IF (year during which animals are to be
               harvested):
                  HARVEST(p);
               END (harvest year) IF
            END (population) LOOP
            FOR (each population, p):
               IF (year during which animals are to be
               supplemented):
                  SUPPLEMENT(p);
               END (supplement year) IF
            END (population) LOOP
            FOR (each population, p):
               Tally PopulationSize[p];
               IF (population is not extinct AND
               population was not extinct prior year):
// "Extinction" can be defined by the user as the absence of
one sex, or as the population size falling below a specified
lower limit.
                  r[p] = log(PopulationSize[p] /
                  PopulationSizePriorYear[p]);
// Calculate population growth rate ( r ).
               END IF
               IF (not extinct AND PopulationSize[p], N
               > CarryingCapacity[p], K):
                  FOR (each living animal):
                     IF (RAND() > K / N):
// Stochastically kill excess above K.
                        Animal dies;
                     END IF
                  END (each animal) LOOP
               END (N > K) IF
               Tally PopulationSize[p];
               IF (population is extinct):
                  Decrement NumberExtantPopulations[p];
                  IF (population was not extinct in prior
                  year):
                     Set YearExtinct[p] = CurrentYear;
                     IF (population has not been
                     recolonized):
// First extinction
                        Set TimeToExtinction[p] =
                        CurrentYear;
                        Increment
                        NumberOfExtinctions[p];
                     ELSE:
// Re-extinction of population
                        Set TimeToReextinction[p] =
                        CurrentYear –
                        YearOfRecolonization[p];
                     END (recolonized) IF/ELSE
                  END (was not extinct) IF
               ELSE:
// Not extinct
                  IF (population was extinct in prior year):
// Recolonization
                     Set YearRecolonized[p] = CurrentYear;
                     Set TimeToRecolonization[p] =
                     CurrentYear – YearExtinct[p];
                     Increment
                     NumberOfRecolonizations[p];
                  END (was extinct) IF
                  Set YearExtinct[p] = 0;
// Flag for not extinct
               END (extinct) IF/ELSE
               Display PopulationSize[p] on screen graph;
            END (population) LOOP
            FOR (each population, p):
               CALC_GENETIC_METRICS(p);
            END (population) LOOP
         END (year) LOOP
      END (iteration) LOOP
// At this point, the simulation is complete and summary
statistics can be calculated.
      FOR (each population, p):
         Calculate and report means, SDs, and SEs across
         iterations for
            Population growth rate: r[p] = N[CurrentYear]
            / N[PreviousYear]
            TimeToExtinction[p]
            TimeToRecolonization[p]
            TimeToReextinction[p]
         FOR (each year):
            Calculate and output means, SDs, and SEs
            across iterations for:
               Probability of extinction, PE[p]
// SE = SQRT[PE * (1 - PE) / NumberIterations]
               PopulationSize[p]
               GeneDiversity[p]
// Gene Diversity = Heterozygosity expected under Hardy-
Weinberg equilibrium
               ObservedHeterozygosity[p]
// = 1 - mean inbreeding coefficient
               NumberAlleles[p]
               LethalFrequency[p]
         END (year) LOOP
      END (population) LOOP
      Calculate and report within-population means of
      above summary statistics;
      Call program for displaying graphical displays of
      trends in:
         PopulationSize
         GeneDiversity
         Mean inbreeding coefficient (1 -
         ObservedHeterozygosity)
         Probability of population persistence to year
         Probability of extinction in that time interval
      Read in DoAnotherScenario?
      IF (DoAnotherScenario? is FALSE):
         BREAK from scenario LOOP
```

```
    END IF
  END (scenario) LOOP
END PROGRAM VORTEX()

BEGIN FUNCTION
READ_SPECIES_PARAMETERS():
// Get input parameters from keyboard or input file, describing simulation parameters, inbreeding effects, and basic species life history.
  Read in Input/Output file names;
  Read in NumberOfIterations;
  Read in NumberOfYears;
  Read in ExtinctionDefinition;
// Extinction can be defined as no animals of one sex, or as the population size falling below a specified minimum.
  Read in NumberOfPopulations;
  Read in InbreedingGeneticLoad;
  Read in ProportionLoadDueToLethals;
  Read in EVCorrelationBetweenReproductionAndSurvival?;
  IF (NumberOfPopulations > 1):
    Read in EVConcordanceAmongPoulations;
  END IF
  Read in NumberTypesOfCatastrophes;
  Read in Monogamous/Polygynous/Hermaphroditic?;
  Read in FemaleBreedingAge;
  Read in MaleBreedingAge;
  Read in MaximumAge;
  Read in SexRatio at birth;
  Read in MaximumLitterSize;
  Read in DensityDependentBreeding?
// The pseudocode for modeling density dependent breeding is not given below.
END FUNCTION READ_SPECIES_PARAMETERS()

BEGIN FUNCTION
READ_MIGRATION_PARAMETERS():
// Get input population structure and migration patterns.
  Read in MigrationAges;
  Read in MigrationSexes;
  Read in MigrationSurvival;
  Read in MigrationDensity;
  FOR (each population, pSource):
    FOR(each other population, pDestination):
      Read in MigrationProb[pSource][pDestination];
    END LOOP
  END LOOP
END FUNCTION
READ_MIGRATION_PARAMETERS()

BEGIN FUNCTION
READ_POPULATION_PARAMETERS(for population p):
  Read in ProportionFemalesBreeding[p];
  Read in BreedEV[p];
// Environmental variation is specified as a standard deviation.
  Read in Litter size distribution (either as
  MeanLitterSize[p] and SDLitterSize[p] or as the fully
  specified distribution of ProbLitterSize[p][n]);
  FOR (each age, x, up to FemaleBreedingAge ):
    Read in FemaleMortality[p][x];
    Read in FemaleMortalityEV[p][x];
  END (age) LOOP
  FOR (each age, x, up to MaleBreedingAge ):
    Read in MaleMortality[p][x];
    Read in MaleMortalityEV[p][x];
  END (age) LOOP
  FOR (each type of catastrophe, c):
    IF (NumberPopulations > 1):
      Read in GlobalOrLocal[p][c];
    END IF
    Read in CatastropheFrequency[p][c];
    Read in CatastropheBreedSeverity[p][c];
    Read in CatastropheSurvivalSeverity[p][c];
  END (catastrophe) LOOP
  CALC_DETERMINISTIC_GROWTH(p);
// Calculate deterministic population growth rate, generation time, and stable age distribution from mean birth and death rates. Effects of any catastrophes are averaged across years
  Read in ProportionMalesInBreedingPool[p];
// See Note 4.
  IF (initial numbers of animals are to be distributed
  according to the stable age distribution):
    Determine initial numbers of animals in each age-sex class;
// The stable age distribution would rarely assign whole numbers to each age-sex class. Integral numbers are assigned that most closely match the desired distribution.
  ELSE (does not start at stable age distribution):
    FOR (each sex):
      FOR (each age up to MaximumAge):
        Read in initial number of animals;
      END LOOP
    END LOOP
  END (stable age distribution) IF/ELSE
  Read in CarryingCapacity[p] (K);
// K may be specified as a function of year or other parameters. See Note 3.
  Read in KEV[p];
  Read in Harvest[p]?;
  IF (Harvest[p]? = Yes):
    Read in FirstYearHarvest[p], LastYearHarvest[p],
    HarvestInterval[p];
    FOR (each age, x, up to FemaleBreedingAge):
// For harvest, all adults are treated in the same age category.
      Read in NumberFemalesToBeHarvested[p][x];
    END LOOP
    FOR (each age, x, up to MaleBreedingAge):
      Read in NumberMalesToBeHarvested[p][x];
    END LOOP
```

```
    END IF
    Read in Supplement[p]?;
    IF (Supplement[p]? = Yes):
        Read in FirstYearSupplementation[p],
        LastYearSupplementation[p],
        SupplementationInterval[p];
        FOR (each age, x, up to FemaleBreedingAge):
            Read in NumberFemalesToBeSupplemented[p][x];
        END LOOP
        FOR (each age, x, up to MaleBreedingAge):
            Read in NumberMalesToBeSupplemented[p][x];
        END LOOP
    END IF
END FUNCTION
READ_POPULATION_PARAMETERS()

BEGIN FUNCTION
CALC_DETERMINISTIC_GROWTH(for population p):
// Use standard life table analysis; solve the Euler equation to find the deterministic growth rate.
    Set fecundity, M = MeanLitterSize[p] * (1 - SexRatio);
// SexRatio is proportion males at birth.
    FOR (each type of catastrophe, c):
// Adjust M for catastrophes.
        Multiply M by CatastropheFrequency[p][c] *
        CatastropheBreedSeverity[p][c] + (1 -
        CatastopheFrequency[p][c]);
    END (catastrophe) LOOP
    FOR (each age, x):
        Set female survival, P[x] = 1 - FemaleMortality[p][x];
        FOR (each type of catastrophe, c):
// Adjust P[x] for catastrophes.
            Multiply P[x] by CatastropheFrequency[p][c] *
            CatastropheSurvivalSeverity[p][c] + (1 -
            CatastopheFrequency[p][c]);
        END (catastrophe) LOOP
        Multiply cumulative survivorship, L[x], by P[x];
        IF (x >= FemaleBreedingAge):
            Add L[x] * M to SumLxMx;
            Add x * L[x] * M to SumAgeLxMx;
        END IF
    END (age) LOOP
    Set R0 = SumLxMx;
    Set GenerationTime[p] = SumAgeLxMx / SumLxMx;
// Preliminary estimate
    Set Lambda = R0 ^ (1/GenerationTime);
// Preliminary estimate
    Solve Euler equation by iterative approximation, to yield precise Lambda;
    Set r[p] = log(Lambda);
    Set GenerationTime[p] = log(R0) / r[p];
    FOR (each age, x):
// Determine stable age distribution.
        Set StableAgeClassSize[p][x] = (1 - SexRatio) * L[x] /
        (Lambda ^ x);
        Add StableAgeClassSize[p][x] to
        SumStableAgeClassSize[p];
    END LOOP
// Repeat age distribution calculations for males, but use female-based Mx and Lambda.
    FOR (each age, x):
        Set male survival, P[x] = 1 - MaleMortality[p][x];
        FOR (each type of catastrophe, c):
// Adjust P[x] for catastrophes.
            Multiply P[x] by CatastropheFrequency[p][c] *
            CatastropheSurvivalSeverity[p][c] + (1 -
            CatastopheFrequency[p][c]);
        END (catastrophe) LOOP
        Multiply cumulative survivorship, L[x], by P[x];
    END LOOP
    FOR (each age, x):
// Determine stable age distribution.
        Set StableAgeClassSize[p][x] = SexRatio * L[x] /
        (Lambda ^ x);
        Add StableAgeClassSize[p][x] to
        SumStableAgeClassSize[p];
    END LOOP
    FOR (each age, x, and sex, s):
        Divide StableAgeClassSize[p][s][x] by
        SumStableAgeClassSize[p];
    END LOOP
END FUNCTION
CALC_DETERMINISTIC_GROWTH()

BEGIN FUNCTION GLOBAL_EV_RANDS():
    FOR (each type of catastrophe):
        Set GlobalCatastropheRand = RAND();
// Select random number to determine if global catastrophe occur. See Note 5.
    END (catastrophe) LOOP
    Set GlobalBreedEVRand = RAND();
// Select random number for specifying EV in breeding for that year.
    Set GlobalBreedEVNRand = NRAND();
// Select random normal deviate for specifying EV in breeding for year. Whether EVRand or EVNRand will be used depends on the magnitude of EV. See Note 6.
    Set GlobalBreedEVNRand to same sign as
    GlobalBreedEVRand;
    IF (EVCorrelationBetweenReproductionAndSurvival? =
    No):
        Set GlobalMortEVRand = RAND();
// Select random 0-1 number for specifying EV mortality for that year.
        Set GlobalMortEVNRand = NRAND();
// Select random normal deviate for specifying EV in mortality for that year. Whether EVRand or EVNRand will be used depends on the magnitude of EV.
        Set GlobalMortEVNRand to same sign as
        GlobalMortEVRand;
        Set GlobalKEVNRand = NRAND();
```

```
// Select random normal deviate for specifying EV in K for year.
   ELSE (EV in breeding is correlated with EV in mortality):
      Set GlobalMortEVRand = GlobalBreedEVRand;
      Set GlobalMortEVNRand = GlobalBreedEVNRand;
      Set GlobalKEVNRand = GlobalBreedEVNRand;
   END (EV correlation) IF/ELSE
END FUNCTION GLOBAL_EV_RANDS()

BEGIN FUNCTION LOCAL_EV_RANDS():
   Set LocalBreedEVRand = RAND();
// Select random number for specifying EV in breeding for year.
   Set LocalBreedEVNRand = NRAND();
// Select a random normal deviate for specifying EV in breeding.
   Set LocalBreedEVNRand to same sign as
   LocalBreedEVRand;
   IF (EVCorrelationBetweenReproductionAndSurvival? =
   FALSE):
      Set LocalMortEVRand = RAND();
// Select random number for specifying EV in mortality.
Set LocalMortEVNRand = NRAND();
// Select random normal deviate for specifying EV in mortality.
      Set LocalMortEVNRand to same sign as
      LocalMortEVRand;
      Set LocalKEVNRand = NRAND();
// Select random normal deviate for specifying EV in K.
   ELSE (EV in breeding is correlated with EV in mortality):
      Set LocalMortEVRand = LocalBreedEVRand;
      Set LocalMortEVNRand = LocalBreedEVNRand;
      Set LocalKEVNRand = LocalBreedEVNRand;
   END (EV correlation) IF/ELSE
END FUNCTION LOCAL_EV_RANDS()

BEGIN FUNCTION CATASTROPHES(for population p):
   FOR (each type of catastrophe, c):
      IF (Catastrophe is local in effect):
         IF (RAND() < CatastropheFrequency[p][c]):
// See Note 5.
            Set CatastropheFlag[c] = TRUE;
// Catastrophe has occurred.
         ELSE:
            Set CatastropheFlag[c] = FALSE;
         END (catastrophe) IF/ELSE
      ELSE:
         IF (GlobalCatastropheRand <
         CatastropheFrequency[p][c]):
            Set CatastropheFlag[c] = TRUE;
         ELSE:
            Set CatastropheFlag[c] = FALSE;
         END (catastrophe) IF/ELSE
      END (Local/Global catastrophe) IF/ELSE
   END (catastrophe) LOOP
END FUNCTION CATASTROPHES()

BEGIN FUNCTION BREED(for population p):
// Find breeders for the year ...
   FOR (each living animal in the population):
      IF (sex = female AND age >= FemaleBreedingAge):
         Add female to breeding pool;
      END IF
      IF (not hermaphroditic):
         IF (sex = male AND age >= MaleBreedingAge):
            IF (RAND() <
            ProportionMalesInBreedingPool[p]):
               Add male to breeding pool;
            END IF
         END IF
      END IF
   END (animal) LOOP
   IF (no males selected for breeding pool, but adult males do exist):
      Add one male at random to breeding pool;
   END IF
   IF (monogamous):
      FOR (each male in breeding pool, m):
         Set MaleUsed[m] = FALSE;
// Flag to indicate male is available for pairing
      END LOOP
   END IF
   IF (hermaphroditic):
      IF (only one breeding female AND
      ProportionSelfing[p] = 0):
         EXIT BREED();
      END IF
   END IF
   FOR (each female, Dam, in breeding pool):
      Let BreedRand = RAND();
      GETBREEDRATE();
// BreedRate is probability of breeding for the female, given by the user either as a constant, ProportionFemalesBreeding, or as a function of population size and other parameters. See Note 3.
      IF (BreedRate = 0):
         CONTINUE LOOP with next breeding female
      END IF
// Find a mate ...
      IF (hermaphroditic):
         IF (RAND() < ProportionSelfing[p]):
            Let Sire = Dam
         ELSE
            Choose a Sire at random from breeding pool;
            WHILE (Sire is Dam):
               Choose a new Sire;
            END WHILE
         END (selfing) IF/ELSE
      ELSE (not hermaphroditic):
         Choose a Sire at random from the male breeding pool;
```

```
        IF (monogamous):
          WHILE (MaleUsed[Sire]):
            Choose a new Sire;
          END WHILE
          Set MaleUsed[Sire] = TRUE;
// Flag Sire as unavailable for future Dams
        END IF
      END IF/ELSE
// Find the litter size for that pairing ...
      IF (MaximumLitterSize > 0):
        Set CumulativeProbLitterSize[0] = 1 - BreedRate;
        FOR each possible litter size, n:
          Set CumulativeProbLitterSize[n] =
          CumulativeProbLitterSize[n - 1]
          + ProbLitterSize[p][n] * BreedRate;
        END LOOP
        FOR (each litter size, n, in decreasing order):
          IF (BreedRand > CumulativeProbLitterSize
          [n - 1] ):
            Set LitterSize = n;
            BREAK from Litter Size LOOP
          END IF
        END LOOP
      ELSE:
// MaximumLitterSize = 0 is a code for using normal distribution of litter sizes.
        Set LitterSize = MeanLitterSize[p] +
        SDLitterSize[p] * NRAND();
        Set LitterSize = max(0, LitterSize);
        Set LitterSize = min(2 * MeanLitterSize[p],
        LitterSize );
// Truncates symmetrically to avoid creating bias.
        Set IntegerLitter = Largest integer less than
        LitterSize;
        Set Remainder = LitterSize - IntegerLitter;
        IF (RAND() < Remainder):
// Round-off litter size probabilistically.
          Set LitterSize = IntegerLitter + 1;
        ELSE:
          Set LitterSize = IntegerLitter;
        END IF/ELSE
      END IF/ELSE
// Create the offspring ...
      Set Inbreeding = Kinship between Sire and Dam;
      FOR (Offspring from 1 to LitterSize):
        Assign ID, age (= 0), population, alive (= TRUE);
        FOR (each of six loci):
// First locus is neutral, others can have lethals.
          Pick at random an allele from Dam;
          Pick at random an allele from Sire;
        END LOOP
        IF(not hermaphroditic AND RAND() <
        SexRatio):
          Assign sex as male;
        ELSE:
          Assign sex as female;
        END IF/ELSE
// Does offspring live? Offspring mortality is placed here in the code, rather than in the MORTALITY() function, for better speed and lower memory requirements.
        FOR (each non-neutral locus):
          IF (homozygous AND allele is a lethal):
            Offspring dies;
          END IF
        END LOOP
        IF (not yet dead):
          GETDEATHRATE();
          Set SurvivalRate = 1 - DeathRate;
          IF (Inbreeding > 0):
            Set SurvivalRate = exp(-0.50 *
            LethalEquivalents * Inbreeding);
          ENDIF
          IF (RAND() > SurvivalRate):
            Offspring dies;
          END IF
        END IF
        IF (not dead):
          Calculate kinship to every living animal;
// See Ballou (1983) for the method of calculating inbreeding and kinship coefficients.
        END IF
      END (offspring) LOOP
    END (breeding females) LOOP
END FUNCTION BREED()

BEGIN FUNCTION GETBREEDRATE():
    Obtain BreedRate by evaluating fecundity function for
    population and individual parameters;
// Most often, the fecundity function will simply return ProportionFemalesBreeding entered by the user. VORTEX provides the option, however, of making breeding a function of PopulationSize, GeneDiversity, Inbreeding, and other variables. See Note 3.
    ADJUSTRATE(BreedRate, LocalBreedEV[p],
    LocalBreedEVRand, LocalBreedEVNRand);
// Adjust rate for local EV.
    ADJUSTRATE(BreedRate, GlobalBreedEV[p],
    GlobalBreedEVRand, GlobalBreedEVNRand);
// Adjust rate for global EV.
    FOR (each type of catastrophe, c):
      IF (CatastropheFlag[c] = TRUE):
        Multiply BreedRate by
        CatastropheBreedSeverity[p][c];
      END IF
    END LOOP
END FUNCTION GETBREEDRATE()

BEGIN FUNCTION MORTALITY(for population p):
    FOR (each living animal in the population):
      IF (age > 0):
// Infant mortality occurs within the BREED() function, not here.
```

```
        IF (at maximum age):
          Animal dies;
        ELSE:
          GETDEATHRATE();
          IF (RAND() < DeathRate ):
            Animal dies;
          END IF
        END IF/ELSE
      END (age > 0) IF
    END (animal) LOOP
END FUNCTION MORTALITY()

BEGIN FUNCTION GETDEATHRATE():
    Obtain DeathRate by evaluating mortality function for
    population and individual parameters;
// Most often, the mortality function will simply return the
mortality rate entered by the user for the age and sex of the
current animal. VORTEX provides the option, however,
of making mortality a function of PopulationSize,
GeneDiversity, Inbreeding, and other variables.
    ADJUSTRATE(DeathRate, LocalMortEV[p],
    LocalMortEVRand, LocalMortEVNRand);
// Adjust rate for local EV.
    ADJUSTRATE(DeathRate, GlobalMortEV[p],
    GlobalMortEVRand, GlobalMortEVNRand);
// Adjust rate for global EV.
    FOR (each type of catastrophe, c):
      IF (CatastropheFlag[c] = TRUE):
        Let DeathRate = 1 -
        (CatastropheSurvivalSeverity[p][c] *
        (1 - DeathRate));
      END IF
    END LOOP
END FUNCTION GETDEATHRATE()

BEGIN FUNCTION ADJUSTRATE(Rate, EV, EVRand,
EVNRand);
    Determine binomial parameter n for modeling EV;
// See Note 6.
    IF (n < 26):
// Find the adjusted Rate from binomial EV.
      FOR (each BinomialOutcome 0 through n):
        Add BinomialOutcome / n to BinomialProportion;
        Calculate BinomialProbability for
        BinomialProportion;
        Add BinomialProbability to CumulativeBinomial;
        IF ( EVRand < CumulativeBinomial ):
          Set Rate = Binomial Proportion;
          BREAK from LOOP
        END IF
      END LOOP
    ELSE:
// Use Normal distribution for EV, and truncate symmetri-
cally to avoid bias.
      IF (Rate > 0.5):
        Set UpperLimit = 1;
        Set LowerLimit = Rate - (1 - Rate);
      ELSE:
        Set UpperLimit = 2 * Rate;
        Set LowerLimit = 0;
      END IF/ELSE
      Add EV * EVNRand to Rate;
      Let Rate = max(LowerLimit, Rate);
      Let Rate = min(UpperLimit, Rate);
    END IF/ELSE
END FUNCTION ADJUSTRATE();

BEGIN FUNCTION MIGRATE():
    FOR (each living animal):
      IF (not in age range that migrates):
        CONTINUE LOOP with next animal;
      END IF
      IF (not a sex that migrates):
        CONTINUE LOOP with next animal;
      END IF
      Set MigrationRand = RAND();
      Set pSource to population of current animal;
      IF ( MigrationRand > CumulativeMigrationProb
      [pSource][NumberPopulations] ):
        CONTINUE LOOP with next animal;
// Does not migrate
      END IF
      Obtain MigrationDensity by evaluating function, or
      using specified constant parameter;
// See Note 3.
      IF (PopulationSize[pSource] / CarryingCapacity
      [pSource] < MigrationDensity ):
        CONTINUE LOOP with next animal;
      END IF
      Obtain MigrationSurvival by evaluating function, or
      using specified constant parameter;
// See Note 3.
// Find to which population the animal migrates ...
      FOR (up to 10 attempts to enter another
      population):
// The limit of 10 attempts is imposed to prevent an infi-
nite loop from occurring when all populations are at carry-
ing capacity.
        IF (RAND() > MigrationSurvival ):
          Animal dies;
          BREAK from LOOP, CONTINUE with
          next animal;
        END IF
        FOR (each population, pDestination):
          IF ( MigrationRand < CumulativeMigrationProb
          [pSource][pDestination] ):
            BREAK from LOOP;
// Animal will try to migrate to pDestination
        END IF
      END LOOP
      IF (Population pDestination at carrying capacity):
        IF (tried 9 times before to find an open population):
```

```
            Animal dies;
// Never found an open population into which to migrate.
            BREAK from LOOP, CONTINUE with
            next animal;
          END IF
          IF (CumulativeMigrationProb[pDestination]
          [NumberPopulations] = 0):
            Animal dies;
// Cannot migrate away from pDestination.
            BREAK from LOOP, CONTINUE with
            next animal;
          END IF
          Set MigrationRand = RAND();
          Set pSource = pDestination;
// Moves on from population pDestination , old pDestination
becomes current pSource.
          WHILE (MigrationRand >
            CumulativeMigrationProb[pSource]
            [NumberPopulations]):
            Set MigrationRand = RAND();
// Must migrate somewhere, so draw a new random
number.
          END WHILE
        END IF
      END LOOP
      Change animal's population to pDestination;
      Adjust tallies of population sizes;
// Increment size of pDestination , decrement size of pSource.
  END animal LOOP
END FUNCTION MIGRATE()

BEGIN FUNCTION HARVEST(for population p):
  FOR (each age, x):
// HARVEST() lumps all animal above breeding age as a
single class.
    IF (NumberMales[p][x] <=
    NumberMalesToBeHarvested[p][x]):
      All males age x die;
    ELSE
      WHILE (number harvested <
      NumberMalesToBeHarvested[p][x]):
        Choose at random a living male in age class x;
        Male dies;
      END WHILE
    END IF/ELSE
  END LOOP
  FOR (each age, x):
    IF (NumberFemales[p][x] <=
    NumberFemalesToBeHarvested[p][x]):
      All females age x die;
    ELSE
      WHILE (number harvested <
      NumberFemalesToBeHarvested[p][x] from age class):
        Choose at random a living female in age class x;
        Female dies;
      END WHILE
    END IF/ELSE
  END LOOP
  Adjust tallies of population size;
END FUNCTION HARVEST()

BEGIN FUNCTION SUPPLEMENT(for population p):
  FOR (each age, x, up to MaleBreedingAge):
    WHILE (number males created <
    NumberMalesToBeSupplemented[p][x]):
      Create a male, assigning ID, age, sex, alleles,
      population;
      Set kinships to all other animals = 0;
      Set Inbreeding = 0;
    END WHILE
  END LOOP
  FOR (each age, x, up to FemaleBreedingAge):
    WHILE (number females created <
    NumberFemalesToBeSupplemented[p][x]):
      Create a female, assigning ID, age, sex, alleles,
      population;
      Set kinships to all other animals = 0;
      Set Inbreeding = 0;
    END WHILE
  END LOOP
END FUNCTION SUPPLEMENT()

BEGIN FUNCTION CALC_GENETIC_METRICS(for
population p):
  FOR (each living animal in the population):
    Increment NumberAlleleCopies[a] for each of the
    two alleles, a, at a neutral locus;
    IF (allele 1 is same as allele 2):
      Increment NumberHomozygotes;
    END IF
  END LOOP
  FOR (each allele, a, of the neutral locus):
    IF ( NumberAlleleCopies[a] > 0 ):
      Increment NumberExtantAlleles;
      Add 0.25 * (NumberAlleleCopies[a] /
      PopulationSize[p]) * (NumberAlleleCopies[a]
      / PopulationSize[p]) to ExpectedHomozygosity[p];
    END IF
  END LOOP
  Set GeneDiversity[p] = 1 – ExpectedHomozygosity[p];
  Set ObservedHeterozygosity[p] = 1 - (NumberHomozygotes /
  PopulationSize[p]);
  FOR (each living animal in the population):
    FOR (each non-neutral locus):
      IF (allele 1 at the locus is a lethal):
        Increment NumberLethals;
      END IF
      IF (allele 2 at the locus is a lethal):
        Increment NumberLethals;
      END IF
    END locus LOOP
  END animal LOOP
```

Set *LethalFrequency[p]* = *NumberLethals* / *PopulationSize[p]*;
END FUNCTION CALC_GENETIC_METRICS()

Note 1: Random integers from 0 to 64K are generated by the algorithm given by Kirkpatrick and Stoll (1981). The C code was modified from Maier (1991). Random real numbers between 0 and 1 are produced by first generating a random integer between 0 and 64K, and then dividing that integer by 64K. Random numbers from a normal distribution, with mean = 0 and SD = 1 are generated by the polar algorithm supplied by Latour (1986). Binomially distributed numbers are generated by first calculating the cumulative probability distribution for the discrete outcomes of the desired distribution, then generating a random real number, and then assessing which binomial outcome covers the portion of the distribution encompassing the random real number.

Note 2: VORTEX asks for the effects of inbreeding to be entered as a number of "lethal equivalents" per diploid animal, with further specification of what proportion of this genetic load is due to recessive lethal alleles vs other genetic effects (such as overdominance). Recessive lethal alleles are modeled such that the death of animals homozygous for lethal alleles will reduce the frequency of the lethals and thereby reduce the average effects of future inbreeding. The proportion of inbreeding depression not due to lethal alleles is modeled as an impact on fitness that follows a negative exponential equation (Morton et al. 1956), and is not reduced during generations of inbreeding.

Note 3: For rates which can be specified as functions of age, sex, inbreeding, population size, gene diversity, year, and population, the rate to be used is determined by evaluating the function specified by the user. If the user enters a fixed constant for the rate, as is usually the case, then the function simply returns that constant. However, the user can specify a mathematical formula that defines a demographic rate as being density-dependent, or a function of other population parameters. For example, fecundity could be specified to decline in older age classes, adult mortality could be specified to increase with inbreeding, or habitat (carrying capacity) could be specified to decrease over time. The algorithms for parsing and evaluating user-defined rate functions (e.g., the first step of functions GETBREEDRATE() and GETDEATHRATE()) are not given in the pseudo-code.

Note 4: The proportion of males in the breeding pool can be entered directly, or indirectly in the form of the proportion of males that breed or as the average number of litters per breeding male. If the proportion in the breeding pool is given indirectly, VORTEX will assume that the distribution of male reproductive success follows a Poisson distribution. The proportion of males in the breeding pool is then calculated by solving the following equations for the unknowns:

LittersPerMale = *ProportionFemalesProducingLitters* * (*NumberAdultFemales* / *NumberAdultMales*) [Note: Adult sex ratio is determined from stable age distribution.]

LittersPerMale = *ProportionMalesInBreedingPool* * *LittersPerMaleInBreedingPool*

ProportionMalesBreeding = *ProportionMalesInBreedingPool* * (1 - exp(-*LittersPerMaleInBreedingPool*))

This last equation adjusts for the fact that in any given year some males in the breeding pool will not happen to be successful breeders (the zero class of the Poisson distribution).

Note 5: The occurrence of probabilistic events is determined by a random number generator. The event is deemed to occur if a random number between 0 and 1 is less than the probability of occurrence for that event.

Note 6: Environmental variation (EV) in breeding and in each mortality rate is modeled as a binomial distribution or as a normal distribution, depending on whether the magnitude of EV is large. The user specifies a mean and standard deviation for each rate. The binomial distribution that has a standard deviation closest to the desired EV is determined by solving the equation for the binomial variance, $V = p * (1 - p) / n$, for the parameter n when given the mean, p, and variance, $V = SD^2$. The parameter n is then rounded to the nearest whole number. If $n < 26$, the binomial distribution with parameters p and n is used for EV. Because of the rounding step necessary to produce the discrete binomial distribution, this distribution will often have a slightly different variance than that entered by the user. If $n > 25$, the normal distribution with mean p and variance V will be used to model EV. In such cases, the normal distribution very closely approximates the binomial distribution.

The binomial distribution is restricted to the interval 0 to 1, and it fits well the distribution of demographic rates across years observed in some natural populations (e.g., Lacy 1993). The PVA program INMAT (Mills and Smouse 1994) uses the related beta distribution for this purpose, and it too is restricted to the biologically meaningful 0 to 1 interval. In contrast, the normal distribution extends infinitely in both directions, although the tails beyond 0 and 1 are typically very small in those cases for which VORTEX uses a normal distribution to model EV. For example, if $p = 0.5$ and $SD = 0.1$ (so that the binomial parameter $n = 25$, the limiting case for VORTEX to use the normal approximation), then the area of the normal distribution outside of the 0-1 range is < 0.000001. When modelling EV as a normal distribution, the distribution must be truncated at 0 and 1. To avoid creating any bias in the mean demographic rate as a result of this truncation, VORTEX always truncates the distribution symmetrically.

For example, if the mean is $p = 0.3$, VORTEX truncates the distribution at 0.0 and 0.6. This truncation will cause the *SD* of the distribution to be very slightly less than that entered by the user.

Some PVA models use continuous distributions such as the normal or log normal to represent EV even when EV is large. In such cases, the necessary truncations can cause EV to be substantially less than intended by the user. Moreover, if the truncation is not symmetric, then the mean demographic rate generated by the model can be strongly biased away from the input parameter.

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Considering threats to the viability of small populations using individual-based models

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As wildlife populations become smaller, the number of interacting stochastic processes which can destabilize the populations increases: genetic effects (inbreeding and loss of adaptability) and instability of the breeding structure (sex ratio imbalances, unstable age distribution, and disrupted social systems) can decrease population growth and stability. Recent analyses have shown that some populations can be very sensitive to these stochastic processes, at larger population sizes than had been suggested previously, and often in unexpected ways. Interactions among processes can reduce population viability much more so than would be assumed from consideration of isolated factors. For example, in monogamous species, random fluctuations in sex ratio will depress the mean number of breeding pairs in populations with as many as 500 adults. At low population densities, individuals may not be able to find mates, or may not encounter individuals sufficiently unrelated to be accepted as suitable mates. Inbreeding depression of demographic rates can become a significant contributor to population decline in populations with several hundred individuals, even if genetic problems are not the primary threat. Most models of genetic decay in small and fragmented populations assume demographic stability. However, when the increases in demographic fluctuations of small populations are considered, rates of loss of genetic variation and accumulation of inbreeding can be much faster than has been suggested before. These processes can be examined in detailed, individual-based PVA models. Accurate data to parameterize these models, however, are often not available. Thus, we need to interpret cautiously PVA conclusions for populations that are small, highly fragmented, or projected for many generations.

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There are many kinds of threats to the viability of populations of wildlife. The processes which have driven many once-abundant populations down to one or few small populations in scattered remnants of habitat include direct exploitation (over-harvest), habitat destruction and fragmentation, degradation of habitat quality, introduction of exotic species, and chains of extinction (Caughley 1994). Often, after precipitous declines occur, conservation biologists and governmental agencies establish recovery actions to try to prevent local extirpation of populations or the ultimate extinction of the taxon.

As wildlife populations become smaller, additional threats to stability and persistence arise, which can exacerbate the difficulty of stopping or reversing a decline. These problems of small populations generally result from stochastic or random processes. In any sampling process, the predictability of an outcome decreases as the sample size is reduced. Many aspects of population dynamics are inher-

ently sampling processes, rather than completely determined events, including: mate acquisition, breeding success, sex determination, transmission of genetic alleles, survival, and dispersal. The uncertainty in such processes can lead to instability in population dynamics. Moreover, fluctuations in demographic and genetic processes cause depression in long-term rates, because the geometric means and other appropriate compound measures of population performance are less than the arithmetic means. Finally, reductions in growth rates and fluctuations in rates can interact synergistically, causing increasing instability and more rapid decline, until the ultimate stability is reached when the population becomes extinct. These processes were termed "extinction vortices" by Gilpin and Soulé (1986), and their examination constitutes the core of most population viability analyses (PVA) (Soulé 1987, Boyce 1992, Lacy 1993/1994).

Caughley (1994) argued that there is a dichotomy in conservation biology, between those who follow a "declining population paradigm," examining deterministic causes of population decline, and those who follow a "small population paradigm," examining the processes that further imperil populations after they have become small. Caughley called for more theory to guide the declining population approach, more data to support the small population approach, and better use of the strengths of the two approaches to guide conservation, but he also questioned whether too much emphasis has been given to small population processes in wildlife conservation. Hedrick et al. (1996) argued that the problems of small populations have at times been under-appreciated, but also that the processes causing population declines and the processes affecting populations that have become small are inter-linked in complex ways, so that PVA and conservation biology must encompass both of Caughley's paradigms.

The problems of small populations have received extensive theoretical treatment (e.g., Soulé 1987), but further assessment of the factors affecting viability of very small populations is needed. I will argue that we often underestimate the importance of these factors in population viability, as the magnitude and even direction of some of these effects may be different than has been commonly supposed. Although I believe that the problems inherent in small populations are more numerous and more severe than is commonly recognized, the same may be true of the causes of population decline. However, because additional threats to population viability arise as populations become small, the kinds of PVA models that are needed for assessing the status and recovery options for a species will change as a species declines. Therefore, it is important to consider carefully which PVA model is most appropriate for a particular analysis (Lindenmayer et al. 1995, Akçakaya and Sjögren-Gulve 2000). An individual-based simulation program that models the stochastic processes of small populations in detail would probably not be the best model for examining viability of a population which numbers in the tens of thousands. Similarly, a population-based structured model which ignores factors such as fluctuations in sex ratio, mate availability, and inbreeding would probably not be the most accurate model for a population which falls below 100 individuals. Many, perhaps all, presently used PVA models assess only some of the threats facing small populations, and therefore may underestimate probabilities of extinction and difficulties in species recovery.

In this paper, I will describe some of the threats to small populations that are not included in most PVA models. This discussion will provide guidance as to when more detailed, individual-based PVA models may be necessary to represent well the dynamics of small populations. Most of the processes I will discuss are particularly important for species with low intrinsic growth rates and stable social systems, and somewhat less so for those with high fecundity and little structure to the social or breeding system. Therefore, these considerations will be most applicable to mammal and bird species, and the bias toward these groups in examples below reflect my greater experience with PVA of these taxa.

Processes destabilizing small populations

Shaffer (1981) categorized the stochastic threats to small populations: demographic stochasticity, environmental stochasticity, natural catastrophes, and genetic stochasticity. These causes of uncertainty and fluctuation in population size interact, but they are conceptually distinct.

Demographic stochasticity

Demographic stochasticity is the random variation in the numbers of births, number of deaths, and sex ratio in a population that results from the fates of individuals being independent outcomes of probabilistic events of reproduction, mortality, and sex determination (Shaffer 1981). The observed variation across years or across populations with constant probabilities would be distributed as binomial distributions. If fates of individuals are independent, then demographic stochasticity is intrinsic to the population, and is a simple consequence of the sampling that occurs as individuals are subjected to the population rates.

Figure 1 shows the percent of whooping cranes *Grus americana* each year from 1938 to 1994 that failed to return the following year to the wintering grounds in Texas. Although some variation in mortality was due to environmental variation and likely catastrophes (see below), most of the variation in survival across years can be accounted for by demographic stochasticity (Mirande et al. 1991). The reduced variation in survival as the population grew in size from 18 birds in 1938 to ca 150 birds in the 1990s is clearly evident.

Demographic stochasticity has been recognized as a

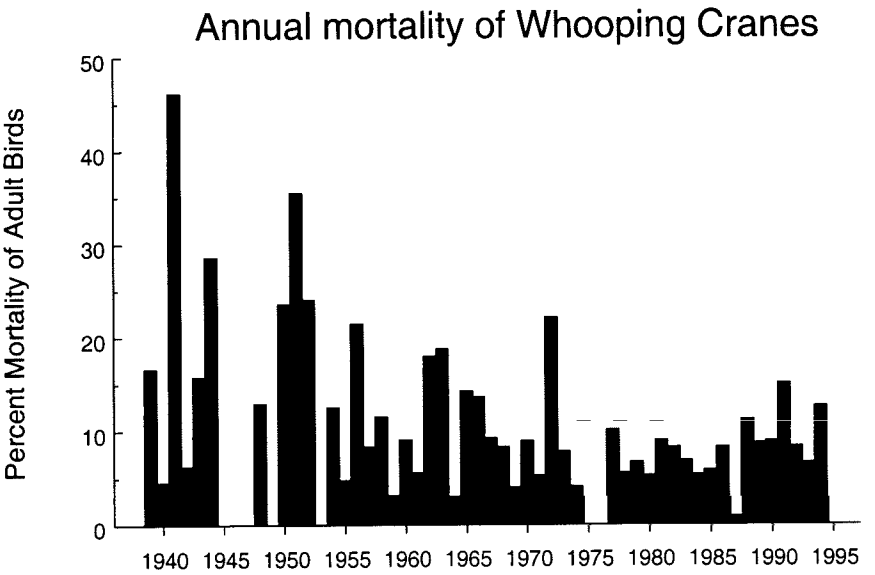

Fig. 1. Percent of whooping cranes observed each year on the wintering grounds which did not survive to return the following year. In years with no bar shown, no birds died. Data from Mirande et al. (1991) and pers. comm.

potential threat to very small populations, but the contribution it can make to population instability has been underestimated. Based on simple calculations of the probability that all individuals will be of the same sex, or die synchronously, it has commonly been stated that demographic stochasticity can cause extinction only when populations fall below ca 10 – 20 individuals (Goodman 1987, Shaffer 1987). However, processes that are not serious problems when acting alone can become significant contributors to population instability and decline when they act synergistically with other threatening processes. The last five dusky seaside sparrows *Ammospiza maritima nigrescens* were all males, an unfortunate but not overly surprising event that effectively eliminated the taxon. The probability that a population of 100 breeders would all be males is essentially zero, so it might be assumed that random fluctuations in sex ratio are unimportant in populations approaching such a size. However, fluctuations in sex ratio can depress population growth significantly, even in such cases. In a population of 100 breeders, we expect ca 50 females and 50 males. But due just to demographic stochasticity, the number of females will deviate by 5 or more (one standard deviation) from this expectation in about one-third of the years. In monogamous species, such as most birds, this means that typically < 50 pairs could be formed. The mean depression in reproduction relative to a population with a constant equal sex ratio can be calculated from the mean absolute deviation of the binomial distribution. Due solely to the random fluctuations in sex ratio, reproduction in a monogamous population with 100 adults would be depressed by ca 8%. This level of reduced population productivity is enough to cause low-fecundity species to switch from positive population growth to long-term population decline and eventual extinction. Brook et al. (1999) found that interaction of the breeding system with fluctuations in the sex ratio strongly influenced projections for population growth of whooping cranes.

Figure 2 shows the mean depression in breeding caused by random variation in the sex ratio for monogamous populations of various sizes. Even with 500 breeding individuals, the mean number of pairs in the population is 3.6% below what would be available if the sex ratio were fixed at 50:50. This simple example of a threat to the viability of small populations illustrates several important points. First, the random deviation in sex ratio does not in itself cause extinction except in the very smallest of populations, but it can interact with other factors such as the breeding system to depress population growth in a vulnerable population sufficiently to cause extinction. Second, it is unlikely that biologists observing the population would recognize that fluctuation in the sex ratio was a contributing cause of lower reproduction and population decline. Third, it would be possible to incorporate the reduction in breeding as an average effect in a simple life table projection. However, to do so requires that the demographic rates were estimated from a population of the size of the population being currently assessed, and that the population remains constant in size. (This last assumption defeats the purpose of PVA.) The effect of biased sex ratios depressing reproduction in monogamous population of changing size could be modeled as a density-dependent effect on reproduction (Stephens and Sutherland 1999, Courchamp et al. 1999). However, I am not aware of any cases in which an analytical or population-based PVA model incorporated the reduction in breeding, as shown in Fig. 2, for monogamous species that would be expected due to sex ratio fluctuations. Many population models ignore sex ratio and breeding system entirely, projecting numbers of females

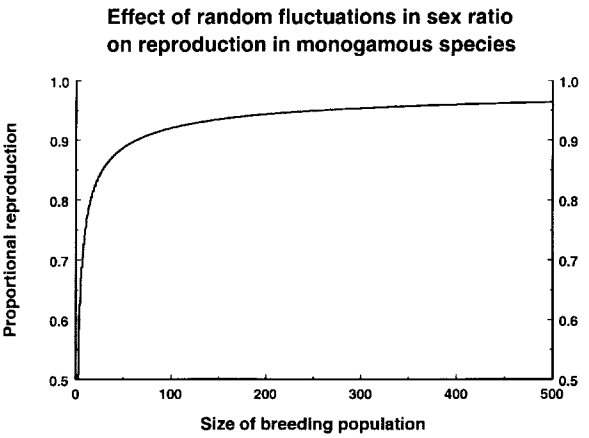

Fig. 2. Mean proportion of monogamous pairs that could be formed relative to the case of a constant 50:50 sex ratio, as a consequence of random fluctuations in the sex ratio in breeding populations of varying size.

under the assumption that there are always males available for mating. Individual-based models are well suited for cases in which sex-ratio biases can disrupt breeding, because they automatically generate stochastic variation in the sex ratio. Rules defining the breeding system can then be built into the model.

Thus, if there is not promiscuous breeding, random fluctuations in the sex ratio can depress population growth in even moderate-sized populations. Similarly, random demographic stochasticity in the numbers of births and deaths per year can depress mean population growth, because of variation in the age distribution and other disruptions of optimal breeding. For example, managers of zoo populations are often distressed to find that reproduction is kept well below optimal levels because of temporary imbalances in the sex ratio or the age distribution. Following the advice of conservation biologists, zoo managers have assumed that a population of 50 or more is safe from the threat of demographic stochasticity, but random fluctuations are causing problems for maintaining stable populations of rhinoceroses, spectacled bears, lions, and other species for which there is limited flexibility to accommodate changes in numbers.

Environmental variation

Environmental variation or stochasticity is the variation in demographic rates or probabilities that results from fluctuations in the environment (Shaffer 1981). Thus, local environmental variation causes temporal clustering of births and deaths, which would increase uncertainty and variability in population size, and thereby make a small population more vulnerable to extinction. The kinds of perturbations of the environment which cause variation in birth and death rates include disease, sporadic predation, irregular food availability, and variable weather. Natural catastrophes are the extreme of environmental variation, in which droughts, floods, fires, disease epidemics, and other local disasters can decimate a population.

Although both demographic stochasticity and environmental variation cause fluctuations in the number of births and deaths in a population, the processes are conceptually distinct and statistically independent. Demographic stochasticity is intrinsic to all populations, regardless of the stability of the environment. As a binomial sampling process, it is highly dependent on the population size. Environmental variation results from variation in habitat quality over time, and is unrelated to population density. The variance in demographic rates caused by environmental variation would be additive with variation due to demographic stochasticity (Goodman 1987).

Environmental variation is not usually affected by the local size of the wildlife population, except in those cases, such as predator-prey interactions, in which the organisms have large effects on their local environment. However, the threat to population viability caused by a given level of environmental variation would be more severe in smaller populations, because smaller populations are closer to extinction. Moreover, the amount of environmental variation would be highly dependent on the total area of habitat occupied by a population. Many environmental stresses are localized, so a population exploiting a large area would benefit from the averaging of any environmental fluctuations that are not synchronous over the entire range. Individuals might use spatial variation in environmental conditions to allow escape from temporal variation in the environment (Kindvall 1996). Even if individuals do not move away from areas with temporarily poor conditions, temporary population declines in some areas would be offset by growth elsewhere.

In PVA models, consideration should be given to whether the amount of environmental variation in the system should change with range contraction and expansion. Unfortunately, data on variation in demographic rates are woefully inadequate for almost all species. Usually, we have no more than crude guesses as to the magnitude of environmental variation for use in population viability analyses. There would be considerable value in a compilation of data across species which would allow generalizations concerning the typical magnitude of fluctuations in demographic rates for species with various life histories, trophic guilds, and habitat types.

Figures 3 and 4 show two examples of fluctuations in natural populations that contrast markedly in the extent to which they are impacted by environmental variation. The population trend for whooping cranes during recovery from a near-extinction shows the reduced relative fluctuations in numbers as the population increased in size. Cranes form long-term monogamous pair bonds, they return to nesting sites for a number of years, they have low fecundity, and they are very long-lived. Hence, they would

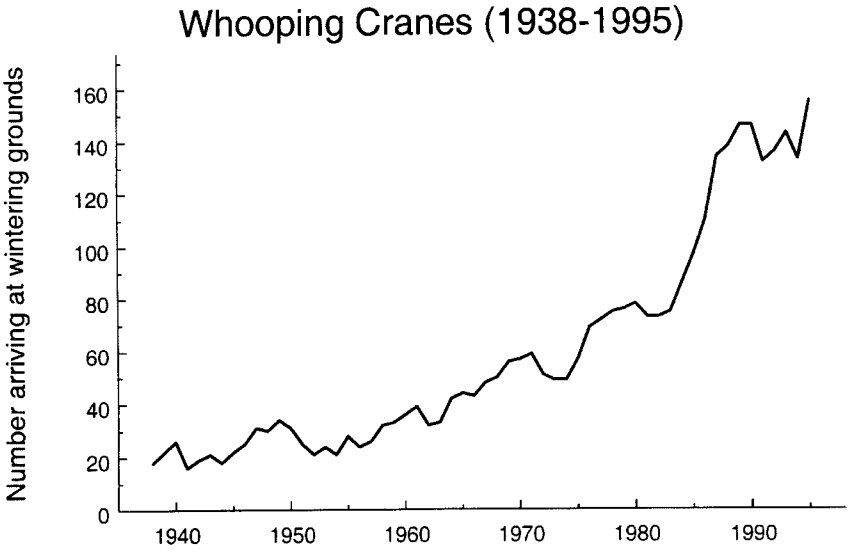

Fig. 3. Number of whooping cranes arriving each winter at the Aransas National Wildlife Refuge, Texas. Data from Mirande et al. (1991).

be expected to show minimal susceptibility to environmental variation. Observed variation in the numbers of hatchlings from 1976 to 1991 was approximately that which would be expected due solely to the demographic variation that would result from a random annual sampling of breeders from the pool of adult birds, each with a constant probability of reproductive success (Mirande et al. 1991). Variation across years in first-year survival was more than three-fold greater than what would be expected due to demographic sampling, indicating that the probability of chick mortality fluctuates across years due to environmental variation. Adult mortality, however, seemed to fall into two classes: in some years, mortality was significantly greater than mortality in other years and deviated significantly further from the mean than can be expected from random demographic stochasticity. The cause of these years of poor survival is not known, as census counts were made only once a year during those years. However, they would appear to be examples of natural catastrophes. If these catastrophe years are excluded from the data as special cases, the annual variation in adult mortality was only slightly greater than that expected due to random demographic stochasticity (Mirande et al. 1991).

Figure 4 shows the population trends for the palila *Loxioides bailleui*, a finch which is restricted to the mamane forests on the slopes of the major volcanoes of the island of Hawai'i. Although some variation in population size may be caused by imprecise census estimates, the species clearly undergoes striking fluctuations in numbers, even though the mean population size is ca 30 times greater than the current population of whooping cranes. Palila must be sensitive to environmental variation, probably

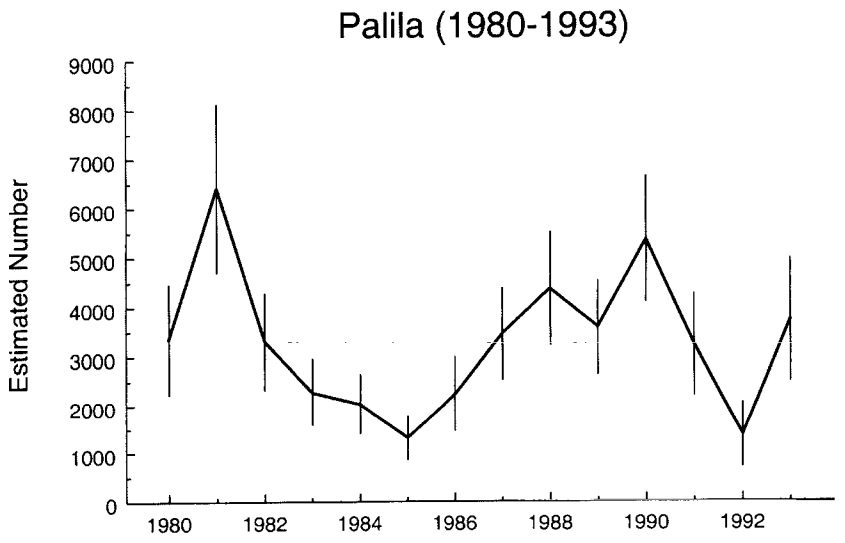

Fig. 4. Estimated numbers of palila, with 90% confidence intervals, from field surveys. Adapted from Ellis et al. (1992).

with respect to both breeding and survival. In part because of the much higher sensitivity to environmental variation, PVA modeling projected a higher probability of extinction for palila (Ellis et al. 1992) than for the much smaller population of whooping cranes (Mirande et al. 1991). The contribution of environmental variation to extinction vortices is well-recognized (Belovsky 1987, Goodman 1987, Foley 1994), but as with demographic stochasticity, we may not always recognize how large the effect can be.

Disrupted breeding systems

There is another cause of demographic instability in small populations, but it does not fit easily within the categories of Shaffer (1981), is rarely considered in PVA models, and may not be fully recognized in conservation plans. At low population densities, the social systems of many species may be disrupted. Such Allee effects are one type of density dependence in reproductive success. Although the importance of understanding and modeling density dependence has been stressed by some authors (Mills et al. 1996, Brook et al. 1997), most of the attention has been given to changes in demographic rates as the population approaches carrying capacity. Yet it is not when a population is near carrying capacity that we need to be concerned about extinction. Allee effects at the low end of density can be incorporated into several of the widely available "generic" PVA models (e.g., RAMAS/Space: Akçakaya and Ferson 1992; VORTEX: Lacy 2000), but this feature seems rarely to be used. Individual-based models can be tailored to provide detailed representations of specific social systems, and this approach was used to look at how the interactions of stochastic processes and pack structure impact viability of wolves (Vucetich et al. 1997) and wild dogs (Vucetich and Creel 1999).

Disruptions of the breeding system can occur for reasons that range from the obvious to the subtle. At very low population densities, animals may be unlikely to encounter any potential mates when they are ready to breed, and non-selfing plants may not be adequately pollinated (Menges 2000). Sumatran rhinoceroses *Dicerorhinus sumatrensis* now exist at densities of only a few per protected area. Field surveys in Malaysia in 1995 found tracks of one juvenile among 35 sets of tracks, and one of 21 adult females captured in the prior decade was pregnant (AsRSG. 1996). If the population were breeding as expected for a rhinoceros species, ca 30% of adult females should be pregnant at any time, and ca 15% of the animals should be under two years of age. Although detailed studies of demography have not been carried out (in part because of the difficulty of studying secretive animals that are at low density in the forest), it is plausible that the scarcity of mates is causing a near cessation of breeding over much of the fragmented range.

Even if some potential mates are available, small populations may provide little opportunity for mate choice. The extent to which a reduced pool of possible mates may be causing breeding delays or failures in small natural populations has not been explored. This problem could be exacerbated if the potential mates are all closely related to the choosing individual or to each other. Ryan (2000) found that, when given a choice of unfamiliar, distantly related females in a Y-apparatus, male *Peromyscus polionotus rhoadsi* mice preferred the less-related female even when differences in kinship averaged only $f = 0.013$, about the level of second cousins. When subsequently paired with one or the other female from the choice test, breeding was delayed and litter sizes were smaller when the only available partner was the one that had been less preferred.

Species with complex social systems may be especially vulnerable to problems resulting from low population density. For example, striped-back wrens *Campylorhynchus nuchalis* have very low breeding success unless they have at least two adult non-breeding helpers sharing in defense against nest-predators, and breeding success is related strongly to the number of such helpers (Rabenold 1990). If such a population were to decline in numbers, recruitment could stop when few birds remained to serve as helpers. One population was rescued from demographic decline when immigrants from nearby populations joined remnant breeding groups (Rabenold et al. 1991). Presumably, extirpation of the local population would have occurred if there had not been nearby sources of immigrants.

Inbreeding depression and loss of genetic diversity

At least two kinds of genetic problems can impact the viability of small populations: reduction of fitness of individuals resulting from inbreeding, and loss of genetic diversity due to random genetic drift (Lacy 1997). There has been much written about (e.g., Frankel and Soulé 1981, Schonewald-Cox et al. 1983, Hedrick and Miller 1992, Frankham 1995a), but also much debate over (e.g., Lande 1988, 1995, Caughley 1994, Caro and Laurenson 1994, Hedrick et al. 1996), the importance of genetics to conservation of wildlife populations.

Inbreeding depression, the reduction in fitness of inbred individuals, frequently occurs when normally outcrossing organisms mate with close relatives. It is commonly believed that it is a problem only for captive populations (which can be substantially buffered from many other risks facing small populations) and for a very few and very small natural populations, or perhaps only as a transient problem that would diminish as selection removes deleterious alleles during repeated generations of inbreeding. Yet, increasing numbers of studies are showing that inbreeding depression can impact population viability to a greater extent, more quickly, and less reversibly than previously supposed (Frankham 1995b, Lacy 1997). Jiménez et al.

(1994) found that inbreeding caused much lower survival of white-footed mice *Peromyscus leucopus* that had been released into a natural habitat than would have been predicted from laboratory measures of inbreeding depression. A population of the greater prairie chicken *Tympanuchus cupido pinnatus*, which had suffered a demographic decline from ca 25 000 birds to < 50 birds over 60 yr, consequently lost substantial genetic variability and suffered reduced fertility and egg viability from inbreeding depression (Westemeier et al. 1998). In Sweden, inbreeding depression of fertility may have been the cause of the rapid decline to extinction of a population of 15 – 20 pairs of the middle spotted woodpecker *Dendrocopos medius* which had been isolated 30 yr before (Pettersson 1985). In Finland, Saccheri et al. (1998) found that local populations of the Glanville fritillary butterfly *Melitaea cinxia* with lower heterozygosity, indicative of greater inbreeding, had lower egg-hatching rate, larval survival, and adult longevity. Apparently as a consequence, these populations had much higher probabilities of extinction.

Following Franklin (1980) and Soulé (1980), only populations with effective sizes below ca 50 have been commonly perceived to be at risk of significant inbreeding depression. To have an effective population size of 50, a typical natural population of a large mammal might need a total population size of ca 200. It is worth reconsidering the likely cumulative effects of inbreeding on the viability of such a population. Inbreeding would accumulate at a rate of 1% per generation. After 10 generations, the 10% cumulative inbreeding may cause a 5% – 20% reduction in survival and in fecundity (Ralls et al. 1988, Lacy et al. 1996, Lynch and Walsh 1998). The consequent reduction in population growth would be sufficient to cause low-fecundity species to decline. Yet, many wildlife managers with responsibility for populations of approximately this size assume that they can ignore effects of inbreeding, and most PVA models for populations of such size omit the impacts of inbreeding on demography.

Many conservation biologists assume that slow inbreeding will not reduce fitness, because selection can remove deleterious alleles during generations of inbreeding (Charlesworth and Charlesworth 1987). Yet, experimental evidence shows that such purging of the genetic load of deleterious alleles from a population often does not work: many populations continue to decline in fitness as they become increasingly inbred (Ballou 1997, Lacy and Ballou 1998) and may go extinct as a consequence (Frankham 1995b). Theoretical work indicates why selection is often ineffective in reducing inbreeding depression. At the small population sizes at which inbreeding occurs, random genetic drift is a much larger force in determining which alleles increase or decrease in frequency than is all but the strongest selection: random loss of adaptive alleles is almost as likely as loss of the deleterious alleles. Except when inbreeding depression is due primarily to a few highly deleterious recessive alleles, inbreeding is more likely to lead to population extinction than to significant reduction of the genetic load (Hedrick 1994). Some populations may be fortunate enough not to carry a genetic load of deleterious alleles which would be expressed under inbreeding, but the evidence suggests that sensitivity to inbreeding may be determined by chance events such as founder effects as much as by any predictable factors (Ralls et al. 1988, Barrett and Kohn 1991, Lacy et al. 1996).

The rate of adaptive evolution of any population is expected to be proportional to its additive genetic variation (and heritability) for the traits under selection (Fisher 1958), and the limited evolutionary potential of domesticated animals with depleted genetic variation has been shown repeatedly. It would be difficult to know whether limited response to selection in rapidly changing habitats is a contributing threat to the persistence of natural populations. Some populations have persisted at small numbers for many generations (e.g., the Javan rhinoceros *Rhinoceros sondaicus*, and, until 1986, the black-footed ferret *Mustela nigripes*), but other populations have rapidly gone extinct when an unusual stress appeared in the environment (e.g., the golden toad *Bufo periglenes* [Pounds and Crump 1994], and the black-footed ferret in 1986 [Clark 1989]). Given the current situation of unprecedented environmental change and an accelerating extinction rate, perhaps more PVA models should consider the maintenance of sufficient genetic variability to ensure ecological and evolutionary flexibility, rather than solely immediate fitness effects and short-term population persistence. One way to accommodate long-term viability into conservation planning would be to use the potential for rapid recovery as the primary measure of population viability, rather than mere population persistence at small numbers. It is also possible to use models that include both the effects of inbreeding on demographic rates and the effects of reduced genetic variability on vulnerability to environmental variation and ability to survive catastrophes. The individual-based model VORTEX (Lacy 2000) can accommodate such dependencies on inbreeding, and similar effects could be built into population-based matrix models as in INMAT by Mills and Smouse (1994). Parameterization of models with genetic-demographic interactions is difficult, but data are increasingly available on the effects of inbreeding on demographic rates (Ralls et al. 1988, Brewer et al. 1990, Saccheri et al. 1998), persistence through environmental stress (Miller 1994, Keller et al. 1994), and population extinction (Frankham 1995b, Saccheri et al. 1998).

Interactions among threatening processes

Although each process described above can individually threaten the viability of small populations, synergistic interactions exacerbate the impacts of many of the processes and are at the center of extinction vortices (Gilpin and Soulé 1986). Interactions among threats are sufficiently

complex that they are often omitted from analytical PVA models and from the functions driving demographic projections in simulation models. Most analytical models are constructed by deriving the impact that a factor would have when acting in isolation from other threatening processes. Below are a few examples of interactions among threatening processes that can reduce population viability, often in unexpected and unexpectedly strong ways.

Increased dispersal among patches of habitat is usually assumed to help stabilize a metapopulation. Increased dispersal can restore genetic variation to previously inbred populations, can reduce demographic fluctuations within local populations, can rescue demographically weak populations (Brown and Kodric-Brown 1977), and can lead to recolonization of temporarily extirpated local populations. However, the metapopulation dynamics of small, partly isolated, and frequently extirpated populations can be highly dependent on spatial, temporal, and behavioral aspects of the population structure (Fahrig and Merriam 1994). For example, if a metapopulation declines to a level at which many of its constituent local populations are very small or extinct, then the benefits of dispersal can be replaced by disadvantages. Uncompensated emigration from isolated populations can depress local population growth (Fahrig and Merriam 1985), and suitable habitat that is temporarily empty can act as a population sink where animals fail to find mates (Gyllenberg and Hanski 1992). Consequently, increased dispersal can accelerate decline of sparsely populated metapopulations (Lindenmayer and Lacy 1995).

This collapse into a metapopulation vortex may be more likely if dispersal behaviors evolved in a physical and biotic environment that was different from the current landscape. For example, in largely contiguous habitat with local competition for breeding territories, the optimal dispersal pattern might be for subadults to always disperse, and to disperse in a random direction. When habitat is highly fragmented and often unoccupied, however, it might be adaptive to remain near the natal site unless local densities are very high (Ronce et al. 2000), and to develop dispersal behaviors that more efficiently locate suitable habitat (for example, habitat with an excess of inhabitants of the opposite sex). Many metapopulations may be occupying recently fragmented landscapes for which their evolved dispersal strategies are suboptimal. In PVA models, it might be important to consider that dispersal strategies that are stabilizing at one population density can become destabilizing at different population densities.

Disruption of breeding systems represents another example of interactions between processes. As populations become small, individuals may become closely related to most or all potential mates. In a number of species, individuals have been observed to avoid mating with genetic relatives (Keane 1990). Inbreeding avoidance in a small population could lead to frequent failures to locate any suitable mates. The suppression of breeding might be considered a form of inbreeding depression, but it may not be recognized as such, since the individuals may all have genotypes that otherwise would confer high fitness, and individuals may not be inbred (in fact, it is the avoidance of inbreeding that causes the depression of fitness). Genetic homogeneity leads to an epiphenomenon, with frequency dependent selection causing the "inbreeding depression" at the population level. Some long-isolated populations of beach mice (such as *Peromyscus polionotus leucocephalus*) have low genetic diversity, low frequencies of breeding when mice are paired in captive colonies, and the poor breeding is increasingly exacerbated when experimental populations are further inbred (Brewer et al. 1990, Lacy and Ballou 1998). It is possible that mate choice behavior that evolved to prevent inbreeding is now often preventing breeding, as the mice breed readily when paired with mice from other subspecies (Lacy unpubl.).

Inbreeding interacts with other threats to population viability. For example, Keller et al. (1994) found that inbred song sparrows *Melospiza melodia* were less likely to survive a severe winter, and inbred animals have occasionally been observed to be more vulnerable to other environmental stresses (Miller 1994).

Not only does demographic decline increase inbreeding, which can in turn further depress mean demographic rates, but smaller populations undergo greater relative demographic fluctuations. The increased fluctuations in numbers depress the genetically effective population size (N_e), as inbreeding and genetic drift are more rapid in a population that fluctuates in size than in a stable population of the same mean size. Together with other factors which can reduce breeding success in smaller populations, this can cause the ratio of the effective population size to the total size (N_e/N) to diminish as a population becomes smaller. Hence, while N_e might be 500 when N = 1000, N_e may be 30 when N = 100, and just 10 when N = 50.

In yet another example of the interaction between genetic and demographic threats to population viability, the joint effects of stochasticity in these two processes have been found to lead to consequences which can be opposite those predicted from purely genetic models. A number of authors have reported that a subdivided population will retain more gene diversity over time than will a single panmictic population, because genetic drift will by chance favor different alleles in the various isolated populations (Boecklen 1986, Varvio et al. 1986, Lacy 1987). However, the models on which this conclusion is based assume that populations are constant in size. The apparently beneficial effect of subdivision is partly due to an artifact of the models, in which model constraints create more equal distribution of reproductive success (and therefore higher N_e) when the population is divided into subunits of fixed size (Barton and Whitlock 1997), and partly due to the protection of different alleles as each subpopulation becomes fixed for a random subset of the diversity of the original metapopulation. This second process can be a benefit of

population subdivision, but it becomes significant only after populations lose most of their gene diversity and become highly inbred, and it depends on no populations becoming extinct as a result of that inbreeding or other factors.

In individual-based PVA models that model genetic changes, the effects of subdivision on gene diversity are quite different, because the PVA models do not unrealistically constrain the populations to be constant in size. Smaller populations undergo greater fluctuations in number and therefore lose gene diversity much faster than if they were part of a larger breeding population. As a consequence of this greater demographic instability, fragmented metapopulations will usually lose genetic variation (both heterozygosity and number of alleles per locus) more rapidly than does a single, more panmictic, large population. This trend occurs even when the effects of fragmentation are partly offset by dispersal among partly isolated populations. In models of populations of mountain brushtail possums *Trichosurus caninus*, Lacy and Lindenmayer (1995) found that both heterozygosity and number of alleles were reduced more quickly when metapopulations of 100 or 200 possums were fragmented into 2, 5, or 10 subpopulations that exchanged up to 5% of their residents each year. Rates of genetic decay slowed as dispersal rates were increased, but the individual-based stochastic model consistently showed that population subdivision caused faster genetic decay from the metapopulation – a result not predicted from many analytical genetic models.

Characteristics of highly vulnerable species

Summarizing this discussion of the threats to viability of small populations, we can identify some of the characteristics of populations that lead to the most complicated population dynamics as populations become small, and which therefore might require the most detailed and individual-based PVA models. Especially vulnerable species would include those with non-breeding helpers, such as striped-back wrens and naked mole rats, species with cooperative foraging, such as many parrots and social carnivores, and species with group defense behaviors, such as musk ox and many primates. Species with precise mechanisms for mate choice, such as many bird species, could have demographic and genetic problems when that choice becomes limited. Monogamous species will have depressed reproduction when there is demographic stochasticity in the sex ratio.

Species with low fecundity are particularly vulnerable to inbreeding depression (Mills and Smouse 1994), because they can withstand less depression of survival before population growth rates become negative and because they will recover more slowly from population bottlenecks. Moreover, of the few PVA models which consider genetic effects (e.g., INMAT: Mills and Smouse 1994; VORTEX: Lacy 2000; and see Menges 2000 for references on plant PVAs), usually an assumption is made that individuals at the start of the population projection are all unrelated and noninbred. Thus, we may under-appreciate existing or imminent genetic problems in populations which have already lost much genetic variation. For example, early analyses of the remnant population of the Florida panther *Felis concolor coryi* assumed that prior inbreeding would not diminish reproductive rates (Seal and Lacy 1989), even though a majority of the males had only one or no functional testicles (Seal et al. 1992). Golden lion tamarins *Leontopithecus rosalia rosalia* are now restricted to very small remnants of the original Atlantic coastal forest of Brazil, have been reduced to a population of ca 350 animals and scattered smaller populations (Ballou et al. 1998), have low genetic diversity (Forman et al. 1986), and show significant depression of juvenile survival when inbred (Dietz et al. 2000). Thus, any PVA models that assume tamarins presently have adequate genetic diversity may project, perhaps incorrectly, that the population could lose much more variation before genetic problems began to reduce population viability.

PVA modeling of small population processes

As illustrated in the examples presented above, more processes threaten the viability of small populations than are commonly addressed in PVA models. Analytical models and simple population projection models can therefore overestimate population growth, underestimate population fluctuations, and seriously underestimate probabilities of extinction. More accurate PVA of small populations may often require individual-based models that simulate interactions among threatening processes rather than relying on theoretical equations derived under assumptions of simplified population processes acting in isolation. Lindenmayer et al. (2000) found that PVA model predictions matched the observed dynamics of populations of three species of marsupials in a highly fragmented landscape only when the models incorporated distance-dependent and density-dependent dispersal, high mortality during dispersal, and spatial variation in habitat quality. Knowledge of times since isolation of each habitat fragment was also critical, as the metapopulations were projected to lose more component subpopulations before reaching extinction-recolonization equilibria. In an alternative approach, Sjögren-Gulve (1994, Sjögren-Gulve and Ray 1996) used a logistic regression model to incorporate similarly detailed information about the habitat characteristics, spatial arrangement, and surrounding forestry practices on the extinction-recolonization dynamics of pool

frog *Rana lessonae* metapopulations. Rather than modeling causal processes, as is done in individual-based models, logistic models can use observed correlates of population transitions to generate predictive models of metapopulation trends. Individual-based models require detailed data on the factors driving population processes, while logistic transition-incidence models require detailed data on the important correlates of population transitions over significant periods of time.

Generalized analytical models can be extremely valuable for discerning many broad trends (e.g., Belovsky 1987), but they do not provide the situation-specific representations that are needed to assess local threats to specific small natural populations nor, usually, the time-specific projections that are needed to understand non-equilibrial systems. Thus, detailed and often individual-based models are more appropriate for comparing management options for endangered species recovery and local conservation planning. We should also retain some skepticism regarding the generality of theoretical results until they have been confirmed to apply to simulated (or, better, real) populations in which the unrealistic assumptions of the theoretical model have been relaxed. There have been recent encouraging confirmations of the ability of PVA models to predict population dynamics (Brook et al. 2000), but more comparisons are needed among analytical results, simulation results from models of varying detail, experimental data, and observations on natural populations.

For a variety of reasons, PVA models for small populations may need to be highly specific with respect to how they model breeding systems, dispersal behavior, and genetic processes. Simple generalizations of population genetics theory may be misleading, because most of that theory was based on large sample approximations. (For example, generalizations about effects of dispersal among small populations often have assumed that an infinite number of such populations exist.) Many metapopulation models assume that the system has reached extinction-recolonization equilibrium. Variation in demographic rates, numbers of individuals, and other population statistics rarely follow a normal distribution. Effects of threatening processes on populations are rarely linear or log-linear, and threshold effects, in which there are sharp discontinuities in effects, are possible. The effects of multiple threats are often synergistic, rather than additive.

Many of the parameters required to build specific, detailed models of small population dynamics can only be estimated well with long-term and extensive data. It is clearly difficult to obtain large samples from small populations, and conservation action may have to precede long-term field studies in order to ensure that the populations persist long enough to permit extended study. Obtaining a complete enumeration of a small population will remove all sampling error in estimation of current parameter values, but it will not necessarily provide sufficiently precise values for predicting future trends. The entire existing population is still only a sample of the universe of all possible populations that could have resulted from the same processes. Given that highly detailed models employing accurate estimates for a large number of parameters might be needed to project the dynamics of small populations well, should PVA models be used to help guide conservation actions? The alternative to using incomplete models with poorly estimated parameters that may overestimate population viability is to use even more general models that will omit many threatening processes and often more seriously underestimate risks, or to rely on intuitive assessments of complex, probabilistic phenomena, something that people are innately poor at doing (Piattelli-Palmarini 1994, Margolis 1996). When planning conservation actions for species that have already declined to near extinction, we should use the best tools available but also recog-

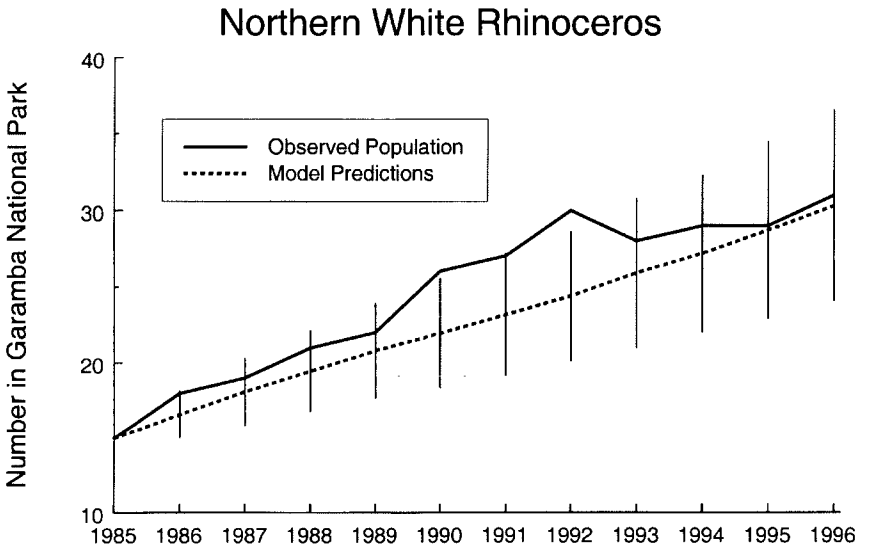

Fig. 5. Observed number (solid line) of northern white rhinoceros in the Garamba National Park, Congo (formerly Zaire), the entire range of the only remaining population of the taxon, and the number projected (dashed line) from the 1985 population. Error bars show the standard deviation across simulations of the projected population size each year. Adapted from Lacy (1996).

nize that our assessments may be crude. Because all PVA models include only a subset of potentially threatening processes, it is possible that many PVAs overestimate viability (Lacy 1993/1994) and that our error will tend to be greatest in the smallest populations – i.e., those which are most critically in need of effective conservation action. Accordingly, margins for error and ongoing monitoring of results should always be part of implementation (see also Akçakaya 2000).

Although the dynamics of small populations can be complex and subjected to many stochastic processes, existing PVA models can provide good representations of dynamics of many such populations. PVA models have predicted well the dynamics of some critically rare species, such as the whooping crane (Brook et al. 1999) and the northern white rhinoceros, *Ceratotherium simum cottoni* (see Fig. 5). Brook et al. (2000) found that PVA models that are sufficiently detailed and for which there are adequate data for estimating parameters can provide unbiased and reasonably accurate predictions for a number of species. The species for which historic population trajectories were modeled in the above studies had been reduced to single populations, rather than existing within metapopulations, and most had relatively simple breeding systems, rather than complex social structures. Also, PVA models may be more reliable when habitat is not limiting population growth than when dynamics near carrying capacity are modeled (Mills et al. 1996, Brook et al. 1997).

How small is small ?

The processes and cases described in this paper suggest that, when it comes to assessing whether wildlife populations have declined to dangerously small sizes, small may be bigger than we usually think it is. Isolated populations with fewer than ca 50 breeding adults may suffer from inbreeding depression within a few generations. Larger populations that are fragmented into partially isolated subunits of fewer than ca 50 breeding animals in each may lose variability much faster than would be estimated from the total metapopulation size (Lacy and Lindenmayer 1995). Genetic decay in populations with fewer than ca 500 breeding adults, or even 5000 adults (Lande 1995), may eventually reduce adaptability and potential for recovery (Lacy 1997). Monogamous species and species with complex social systems may have reduced breeding if numbers fall below several hundred adults. Each of these factors tends to be a greater threat in those species, such as many mammals and birds, that have low fecundity and only slow population growth under optimal conditions.

Finally, it may be difficult to know when a population is so small that additional stochastic factors must be included in a PVA to obtain an accurate projection of its dynamics. Therefore, it is often useful to test several models to determine if added complexity substantially alters PVA predictions, and provides a better fit to observed population trends. A good example of this type of exploration is provided by the ongoing work of Lindenmayer and his colleagues on the fauna of fragmented forests in Australia (Lindenmayer et al. 1999, 2000). PVA models should be no more complex than necessary, but to be useful for conservation they must also be detailed enough to model the real population dynamics accurately (Starfield and Bleloch 1986, Starfield 1997, Akçakaya and Sjögren-Gulve 2000, Lacy and Miller 2001).

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